

The Collected Papers of Ralph Hile 1928-73

Volume I
1928-46

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Washington, D.C.

1977

FOREWORD

The papers collected here include the principal published contributions of Ralph Hile, a highly respected scientist of the U.S. Fish and Wildlife Service and its predecessor, the U.S. Bureau of Fisheries. During a distinguished career in the Federal Government that spanned nearly 40 years, Dr. Hile produced fundamental and pioneering works on such diverse subjects as morphological variation in coregonids; age, growth, abundance, and distribution of freshwater fishes; and methods of statistical analysis and biological interpretation of catch-effort records of the commercial fisheries of the Great Lakes. Some of the most notable of these contributions are standard references that have long been out of print.

Born in Plainville, Indiana, on March 18, 1904, Dr. Hile received an A.B. degree from Indiana Central College in 1924 (and an honorary LL.D. in 1961). He earned his Ph.D. in zoology at Indiana University in 1930, the same year in which he began a career in Federal fishery research that continued until his retirement in 1969.

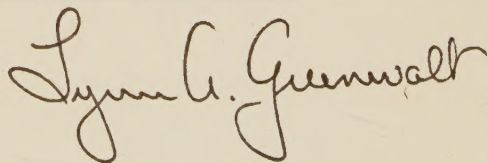
Dr. Hile's earliest activities in his long Government career included the collection of materials from lakes of the northern highlands region of Wisconsin that became the basis for his later classical works on the effect of the environment on the morphometry of the cisco, and on the fluctuations of growth of the rock bass.

He joined the staff of the Great Lakes Fishery Laboratory, Ann Arbor, Michigan, in 1933; was assistant director of the Laboratory in 1958-61; and was named senior scientist in 1962. In 1965 he organized and headed the technical editing unit of the Division of Biological Research of the Bureau of Commercial Fisheries, a position he held until his retirement. During much of his career he contributed his extensive knowledge and experience toward the training of graduate students, while serving as a Research Associate in the Department of Fisheries and Wildlife and the Department of Zoology of the University of Michigan.

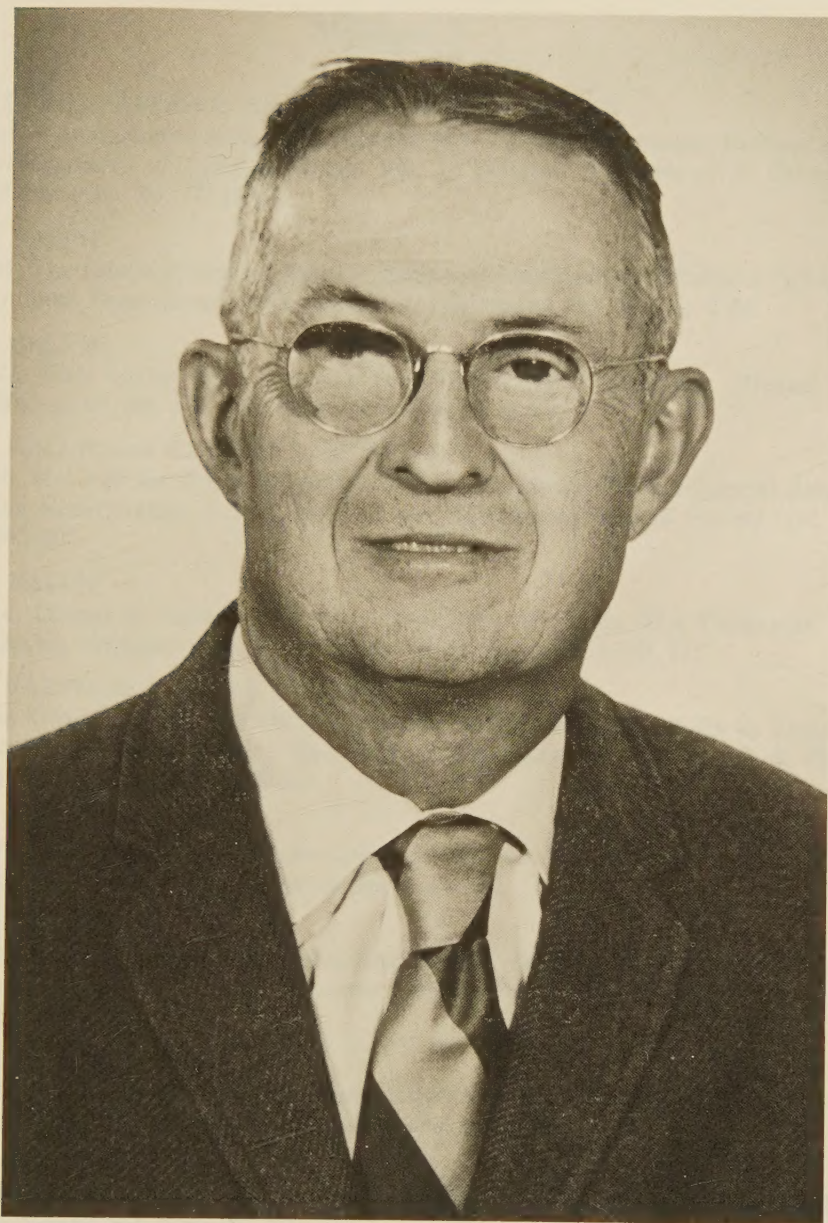
The Department of the Interior's highest honor—the Distinguished Service Award—was conferred on Dr. Hile in 1962 in recognition of his then more than 31 years of outstanding Federal service and his many contributions to the Department's scientific program.

Dr. Hile was a member of a number of professional and scientific organizations, including the American Association for the Advancement of Science, American Fisheries Society, American Society of Limnology and Oceanography, American Society of Zoologists, Biometric Society, and the International Limnological Society. He was a Fellow of the American Institute of Fishery Research Biologists. He was especially active in the American Fisheries Society, of which he became a member in 1932. He was Editor of four annual volumes of the *Transactions of the American Fisheries Society* (1945-48), and was elected President of the Society in 1952 and Honorary Member in 1962. In 1972 he received the Society's Award of Excellence in recognition of his eminent career in fishery research and his services to the Society.

The works that follow are compiled in the order of publication, and thus chronicle a highly productive career that began with a predoctoral study on the bottom fauna of an Indiana Lake in 1928 and has thus far extended to a brief but significant paper on science writing in 1971. The volumes are offered not only to make Dr. Hile's contributions more widely available to present and future fishery biologists everywhere, but also to pay tribute to this most distinguished and admired scientist of the U.S. Fish and Wildlife Service.



Lynn A. Greenwalt, Director
U.S. Fish and Wildlife Service



Ralph Hile



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THE COLLECTED PAPERS OF RALPH HILE

1928-73

Volume I

1. SCOTT, WILL, RALPH O. HILE, and HERMAN T. SPIETH
1928. A quantitative study of the bottom fauna of Lake Wawasee (Turkey Lake). Investigations of Indiana Lakes, No. 1, Indiana Department of Conservation Publication No. 77, 25 pp.
2. HILE, RALPH
1931. The rate of growth of fishes of Indiana. Investigations of Indiana Lakes, No. 2, Indiana Department of Conservation Publication No. 107, pp. 7-55.
3. HILE, RALPH
1932. Fish scales and commercial fisheries. The Fisherman (Grand Haven, Michigan), vol. 1, no. 10 (September), pp. 3, 4, 10.
4. HILE, RALPH, and WILLIAM R. DUDEN
1933. Methods for the investigation of the statistics of the commercial fisheries of the Great Lakes. Transactions of the American Fisheries Society, vol. 63, pp. 292-305.
5. HILE, RALPH
1934. Causes of variation in the growth rates of fishes. The Fisherman (Grand Haven, Michigan), vol. 3, no. 2 (March-April), pp. 3, 4, 10, 11.
6. HILE, RALPH, and HILARY J. DEASON
1934. Growth of the whitefish, *Coregonus clupeaformis* (Mitchill), in Trout Lake, northeastern highlands, Wisconsin. Transactions of the American Fisheries Society, vol. 64, pp. 231-237.
7. HILE, RALPH
1935. Daily reports reveal new facts and figures. The Fisherman (Grand Haven, Michigan), vol. 4, no. 12 (December), pp. 1, 2.
8. HILE, RALPH
1936. Age and growth of the cisco, *Leucichthys artedi* (Le Sueur), in the lakes of the northeastern highlands, Wisconsin. U.S. Bureau of Fisheries Bulletin, vol. 48, pp. 211-317.
9. HILE, RALPH
1936. Age determination of fish from scales; method and application to fish cultural problems. The Progressive Fish-Culturist, No. 23, pp. 1-5.
10. HILE, RALPH
1936. Low production may not mean depletion. The Fisherman (Grand Haven, Michigan), vol. 5, no. 2 (February), pp. 1, 2.
11. HILE, RALPH
1936. Summary of investigations on the morphometry of the cisco, *Leucichthys artedi* (Le Sueur), in the lakes of northeastern highlands, Wisconsin. Papers of the Michigan Academy of Science, Arts, and Letters, vol. 21 (1935), pp. 619-634.
12. HILE, RALPH
1937. The increase in the abundance of the yellow pike-perch, *Stizostedion vitreum* (Mitchill), in Lakes Huron and Michigan, in relation to the artificial propagation of the species. Transactions of the American Fisheries Society, vol. 66 (1936), pp. 143-159.

13. HILE, RALPH
1937. Morphometry of the cisco, *Leucichthys artedi* (Le Sueur), in the lakes of the northeastern highlands, Wisconsin. Internationale Revue der gesamten Hydrobiologie und Hydrographie, vol. 36, no. 1/2, pp. 57-130.
14. SCOTT, WILL, RALPH HILE, and H. T. SPIETH
1938. The bottom fauna of Tippecanoe Lake. Investigations of Indiana Lakes and Streams, No. 4, Indiana Department of Conservation and Indiana University Biological Station, pp. 3-16.
15. HILE, RALPH
1941. Age and growth of the rock bass, *Ambloplites rupestris* (Rafinesque), in Nebish Lake, Wisconsin. Transactions of the Wisconsin Academy of Sciences, Arts, and Letters, vol. 33, pp. 189-337.
16. HILE, RALPH, and FRANK W. JOBES
1941. Age, growth, and production of the yellow perch, *Perca flavescens* (Mitchill), of Saginaw Bay. Transactions of the American Fisheries Society, vol. 70 (1940), pp. 102-122.
17. HILE, RALPH, and CHANCEY JUDAY
1941. Bathymetric distribution of fish in lakes of the northeastern highlands, Wisconsin. Transactions of the Wisconsin Academy of Sciences, Arts, and Letters, vol. 33, pp. 147-187.
18. HILE, RALPH
1942. Growth of the rock bass, *Ambloplites rupestris* (Rafinesque), in five lakes of northeastern Wisconsin. Transactions of the American Fisheries Society, vol. 71 (1941), pp. 131-143.
19. HILE, RALPH, and FRANK W. JOBES
1942. Age and growth of the yellow perch, *Perca flavescens* (Mitchill), in the Wisconsin waters of Green Bay and northern Lake Michigan. Papers of the Michigan Academy of Science, Arts, and Letters, vol. 27 (1941), pp. 241-266.
20. HILE, RALPH
1943. Mathematical relationship between the length and the age of the rock bass, *Ambloplites rupestris* (Rafinesque). Papers of the Michigan Academy of Science, Arts, and Letters, vol. 28 (1942), pp. 331-341.
21. VAN OOSTEN, JOHN, RALPH HILE, and FRANK W. JOBES
1946. The whitefish fishery of Lakes Huron and Michigan with special reference to the deep-trap-net fishery. U.S. Fish and Wildlife Service, Fishery Bulletin, vol. 50, pp. 297-394.

Volume II

22. HILE, RALPH, and HILARY J. DEASON
1947. Distribution, abundance, and spawning season and grounds of the kiyi, *Leucichthys kiyi* Koelz, in Lake Michigan. Transactions of the American Fisheries Society, vol. 74 (1944), pp. 143-165.
23. DEASON, HILARY J., and RALPH HILE
1947. Age and growth of the kiyi, *Leucichthys kiyi* Koelz, in Lake Michigan. Transactions of the American Fisheries Society, vol. 74 (1944), pp. 88-142.

24. HILE, RALPH
1948. Standardization of methods of expressing lengths and weights of fish. Transactions of the American Fisheries Society, vol. 75 (1945), pp. 157-164.
25. HILE, RALPH
1949. Structure and senses of fish. U.S. Fish and Wildlife Service, Fishery Leaflet 132, 13 pp.
26. HILE, RALPH
1949. Trends in the lake trout fishery of Lake Huron through 1946. Transactions of the American Fisheries Society, vol. 76 (1946), pp. 121-147.
27. VAN OOSTEN, JOHN, and RALPH HILE
1949. Age and growth of the lake whitefish, *Coregonus clupeaformis* (Mitchill), in Lake Erie. Transactions of the American Fisheries Society, vol. 77 (1947), pp. 178-249.
28. HILE, RALPH
1950. A nomograph for the computation of the growth of fish from scale measurements. Transactions of the American Fisheries Society, vol. 78 (1948), pp. 156-162.
29. HILE, RALPH
1950. Green Bay walleyes: A report on the scientific investigation of the marked increase in abundance of walleyes in Green Bay. The Fisherman (Grand Haven, Michigan), vol. 18, no. 3 (March), pp. 5, 6.
30. HILE, RALPH, PAUL H. ESCHMEYER, and GEORGE F. LUNGER
1951. Decline of the lake trout fishery in Lake Michigan. U.S. Fish and Wildlife Service, Fishery Bulletin, vol. 52, pp. 77-95. [Summary in The Fisherman (Grand Haven, Michigan), vol. 19, no. 1 (midwinter issue 1951), pp. 5, 10.]
31. HILE, RALPH, PAUL H. ESCHMEYER, and GEORGE F. LUNGER
1951. Status of the lake trout fishery in Lake Superior. Transactions of the American Fisheries Society, vol. 80 (1950), pp. 278-312. [Summary in The Fisherman (Grand Haven, Michigan), vol. 19, no. 3 (late spring issue 1951), pp. 5, 13.]
32. HILE, RALPH
1952. Changes in the lake trout fishery in the three upper lakes. The Fisherman (Grand Haven, Michigan), vol. 20, no. 6 (early fall issue), pp. 5, 8.
33. HILE, RALPH
1952. Fishing regulations. The Fisherman (Grand Haven, Michigan), vol. 20, no. 3 (early spring issue), pp. 5, 12, 14.
34. HILE, RALPH
1952. 25 years of Federal fishery research on the Great Lakes. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 85, ii + 48 pp.
35. HILE, RALPH
1953. Perch studies in Green Bay. The Progressive Fish-Culturist, vol. 15, no. 3, pp. 133-134.
36. HILE, RALPH
1953. Trout fishing in Michigan waters of Lake Superior, 1952. The Fisherman (Grand Haven, Michigan), vol. 21, no. 5 (summer issue), pp. 7, 11, 12, 14.
37. HILE, RALPH, GEORGE F. LUNGER, and HOWARD J. BUETTNER
1953. Fluctuations in the fisheries of State of Michigan waters of Green Bay. U.S. Fish and Wildlife Service, Fishery Bulletin, vol. 54, pp. 1-34.

38. HILE, RALPH
1954. Changing concepts in fishery research on the Great Lakes. Proceedings of the Gulf and Caribbean Fisheries Institute, Sixth Annual Session, pp. 64-70.
39. HILE, RALPH
1954. Fluctuations in growth and year-class strength of the walleye in Saginaw Bay. U.S. Fish and Wildlife Service, Fishery Bulletin, vol. 56, pp. 7-59.
40. HILE, RALPH
1954. Status and future of the American Fisheries Society. Transactions of the American Fisheries Society, vol. 83 (1953), pp. 357-359.
41. HILE, RALPH
1955. The walleye problem in Green Bay. The Progressive Fish-Culturist, vol. 17, no. 1, p. 44.
42. HILE, RALPH, and HOWARD J. BUETTNER
1955. Commercial fishery for chubs (ciscoes) in Lake Michigan through 1953. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 163, ii + 49 pp.
43. HILE, RALPH
1957. U.S. Federal fishery research on the Great Lakes through 1956. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 226, iii + 46 pp.
44. HILE, RALPH, and HOWARD J. BUETTNER
1959. Fluctuations in the commercial fisheries of Saginaw Bay, 1885-1956. U.S. Fish and Wildlife Service, Research Report No. 51, iv + 38 pp.
45. SMITH, STANFORD H., HOWARD J. BUETTNER, and RALPH HILE
1961. Fishery statistical districts of the Great Lakes. Great Lakes Fishery Commission, Technical Report No. 2, 24 pp.
46. HILE, RALPH
1962. Collection and analysis of commercial fishery statistics in the Great Lakes. Great Lakes Fishery Commission, Technical Report No. 5, ii + 31 pp.
47. HILE, RALPH
1966. U.S. Federal research on fisheries and limnology in the Great Lakes through 1964: An annotated bibliography. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 528, iii + 53 pp.
48. HILE, RALPH
1970. Body-scale relation and calculation of growth in fishes. Transactions of the American Fisheries Society, vol. 99, no. 3, pp. 468-474.
49. HILE, RALPH
1971. No read—no write. Transactions of the American Fisheries Society, vol. 100, no. 2, pp. 394-395.
50. HILE, RALPH
1973. Structure and senses of fish. U.S. National Marine Fisheries Service, Marine Fisheries Review, vol. 35, nos. 5 and 6, pp. 48-53.

INVESTIGATIONS OF INDIANA LAKES

I. A Quantitative Study of the Bottom Fauna of Lake Wawasee (Turkey Lake)

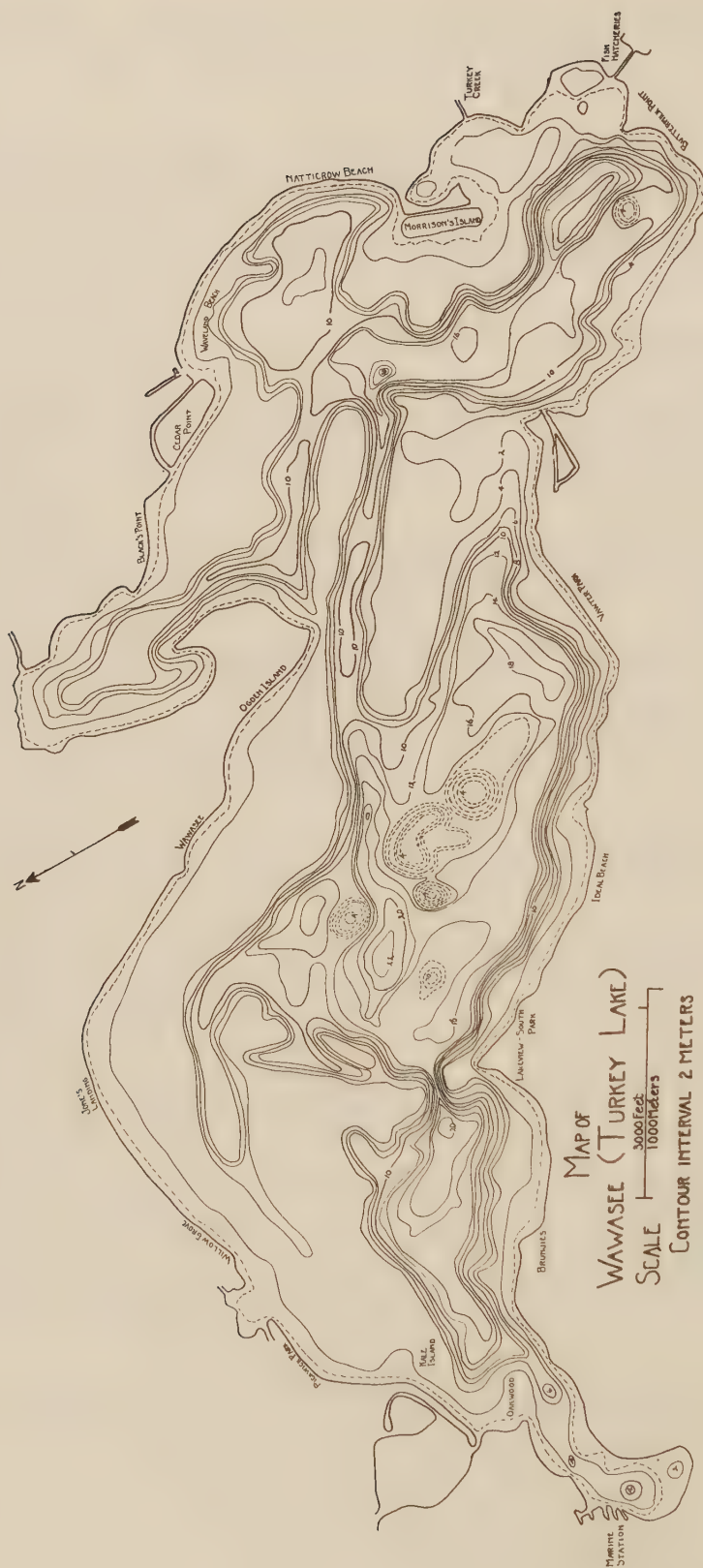
By

WILL SCOTT, RALPH O. HILE, AND HERMAN T. SPIETH

In cooperation with
THE DIVISION OF FISH AND GAME
of the
DEPARTMENT OF CONSERVATION

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THE DEPARTMENT OF CONSERVATION

STATE OF INDIANA

CONSERVATION COMMISSION

STANLEY COULTER, Chairman

EVERETT L. GARDNER, Secretary

DAVID A. ROTHROCK

MARTIN A. GOSHORN

PUBLICATION No. 77

1928

RICHARD LIEBER

Director



PLATE I. A. Cedar Point, one of the promontories having rapid wave erosion and few plants.
 B. Hatcheries Bay, no erosion and many plants.

INTRODUCTION

Early in 1926 the Superintendent of the Division of Fish and Game of the Indiana Department of Conservation and the Director of the Indiana University Biological Station agreed to cooperate in the investigations of the lakes of Indiana, giving especial attention to the fundamental problems related to the fisheries. The Division of Fish and Game pays the field expenses and publishes the results. The University furnishes the apparatus, the men to do the field work, and laboratory facilities for working up the material.

The problem attacked is the productivity of our lakes and the factors that influence it. Studies on other lakes indicate that fishes grow more rapidly in one habitat than in another. The age and consequently the rate of growth of most of our fishes can be determined with considerable accuracy by a study of their scales.

It is planned to estimate as accurately as possible the number of organisms present in a series of lakes and the amount of organic material they contain that is available for fish food. Correlated with this a study is being made of the rate of growth of the fishes in these lakes.

Lake Wawasee (Turkey Lake) was investigated first and the data on this lake form the basis of this report. This lake was selected for two reasons. It is the largest lake in the state and on it the Division of Fish and Game has a hatchery, whose facilities were made available for the field work.

Two summers have been devoted chiefly to the study of the bottom fauna of the lake. The first (1926) was devoted to the littoral (shore) forms out to a depth of two meters. During the second season the deep water organisms were studied. Some preliminary work was done on the dissolved gases and plankton.

The junior authors are responsible for the collecting and counting. The senior author planned the work, supervised its execution, did the weighing, aided in the identification of organisms, and has done most of the subsequent work on the material. Mr. Spieth prepared the map and Mr. Hile has done most of the computing on the morphometry of the lake. The work on fish scales is wholly the work of Mr. Hile. The three of us have conferred at every point in the study and share responsibility for the general results.

The Lake

Location

Lake Wawasee (Turkey Lake) is located in Kosciusko County, Indiana. It lies in sections 8, 9, 10, 11, 13, 14, 15, 16, 17, 22, 23, 24, 25, and 26 R.7E., T.34N. Almost all of section 15 lies in the lake. Of all the sections forming part of the lake this has the maximum water area.

The lake includes the intersection of parallel 41° 31' N. Lat. and the meridian 88° 44' W. Long.

The waters of this lake are a part of the St. Lawrence drainage basin, and are carried through Turkey Creek, Elkhart River, and St. Joseph River to Lake Michigan. It lies near the western edge of the Saginaw Huron-Erie

interlobate moraine. Two miles south of the lake occurs an undissected part of this moraine which forms a part of the continental divide separating the drainage of the St. Lawrence and the Mississippi. Webster Lake, four miles south of Lake Wawasee (Turkey Lake), discharges its water to the Mississippi through Grassy Greek, Tippecanoe Lake, Tippecanoe River, Wabash River, and Ohio River.

Dimensions

The longest axis of the lake is approximately N.W. to S.E. Its greatest length taken as the maximum distance between parallel lines tangent to the lake shore is 22,700 ft. (6,920 m.) or 4.29 miles. Taking the maximum length as the longest mid-channel line, that is, a line from the hatcheries bay to the bay at the west end of the lake, it is 25,300 ft. (7,713 m.) or 4.79 miles.

Considering the first as the maximum length the average width is 5,559 ft. (1,695 m.) or 1.05 miles. If the mid-channel line is considered the maximum length, the average width is 4,982 ft. (1,519 m.) or .94 miles. The greatest length of open water on a straight line is 21,400 ft. (6,920 m.) or 4.05 miles.

The shore line is 15.73 miles (25.33 kilometers) in length.

Form

The determination of the form of a lake is basic to any study of its physical and chemical characteristics or to any quantitative study of the organisms living in it. Not only its outline but depth, areas of various depths and volume must be known. To determine these facts a metric map was constructed based on soundings made by Dr. W. M. Tucker and kindly supplied by him. Certain minor corrections have been incorporated in the map. The metric system has been used in order that these results may be more easily compared with the results obtained on the other lakes of the world.

The general form or contour of the lake can be seen most easily by consulting the map. There are three rather distinct basins, one in the S.E. or hatcheries bay, one toward the west end and a larger and more irregular basin occupying the central portion of the lake.

The east and west basins each reach a depth of 20 meters (66 ft.). The central basin has a maximum depth of 23 meters (76 ft.).

The eastern depth is connected with the central one by a channel which at its narrowest point south of "Ogden's Island," is 140 meters (460 ft.) wide between the 4 meter contours. The depth of this channel is near 10 meters. The channel connecting the west basin with the central one is narrower but reaches a maximum depth of slightly more than 14 meters.

The central basin is not only irregular in outline but contains five shallows where the bottom rises rather rapidly to within four meters (or less) of the surface. Three of these are near each other and separated from the other two by the sixteen meter contour.

Johnson's Bay forms a shallower basin. The eight meter contour encloses quite an area in this bay but the ten meter contour barely reaches the entrance. In the three major basins the oxygen is exhausted from the lower levels but in Johnson's Bay there is a rather large amount of oxygen to the very bottom in spite of the fact that the bottom here is covered with rich

organic debris. It appears from the temperature readings that when the wind sets in from the southeast the water piles up in this bay and forces the bottom water toward the deeper water to the southeast.

Slope

The slope has been computed in per cents, which is another way of saying that it is the average difference in depth in feet for each hundred feet from the shore toward the deeper part of the lake.

The formula used is appended at the end of the paper. The slope between two contours is another way of expressing the distance between them. If the average distance between them is short the slope is steep. It is, of course, related to the area between the contours, and the length of the contours; the longer the contours with a given area the steeper the slope and conversely the greater the area between contours of a given length the more gentle the slope. It will appear that slope is a very important factor in the economy of this lake.

In about twenty other Indiana lakes that have been examined, the slope is less from the shore to the 2 meter contour (S-2) than at any other level. In Lake Wawasee (Turkey Lake) however, this region has a slightly steeper slope than the area between 2m.-4m. contours. The S-2m. slope is 2.42 while the 2m.-4m. slope is only 1.45. Not only is the 2m.-4m. level one of gentle slope but it contains 923 acres or nearly one-third (32.1 per cent) the area of the entire lake. This means that 923 acres of this lake are between 2 meters and 4 meters in depth and slopes on an average less than 1½ feet to the hundred. The data indicate also that this is a very productive area. Fifty-one and nine-tenths (51.9) per cent are less than four meters in depth.

From the depth of four meters, the slope becomes relatively steep until a depth of 8 meters is reached when it again becomes more gentle. The slope from four to six meters is 9.01 and from six to eight meters is 11.84 per cent. The areas contained are 6 per cent and 5.1 per cent, respectively, of the entire lake. To put this graphically, the maximum grade allowed on a federal aid highway is seven per cent. The average slope in this lake between six and eight meters is one and sixty-nine hundredths times this maximum.

The average slope for the whole lake is 4.01. The areas between slopes, the slopes in per cents for each level, and the per cent of the total area included between successive contours are given in Table No. 1.

Volume

The volume of the lake has no very direct relation to the bottom fauna but where the plankton is studied its significance is apparent. While 51 per cent of the area of the lake is above the 4 meter level, slightly less than one-half, 47 per cent of the volume lies above this depth. The ten meter level has 83.5 per cent of the water of the lake above it and 16.5 per cent below it. It is evident that the plankton of the upper levels is the more important. See Table No. 2.

The Collections

Littoral

The lake was divided into littoral and deep water areas at the 2 meter contour. This was done simply for convenience in collecting. In the shallower

water (out to 2 meters) more accurate samples could be obtained with the hoe dredge while beyond this depth the Ekman dredge was used. The summer of 1926 was devoted to the study of the littoral. Two series of collections were made along the shore line. Each series required about six weeks to complete. The fauna changes during the season and it is desirable to complete the series in as short a time as possible. Any method must be a compromise and the plan used is good in that it gives an early summer and a later summer picture.

The littoral stations were spaced according to variations in the habitat rather than equidistant. The stations of the second series alternated with the stations of the first series. Each station was regarded as typical for a definite area.

This area was determined by bisecting the distance between two stations. The area enclosed by the two bisecting lines, the shore, and the 2 meter contours were assigned to the contained station. The areas were determined separately with a planimeter. See Plate No. 5.

It was assumed that the fauna was distributed evenly over each station area. The fauna at each station was determined by averaging collections at four depths, .5m., .75m., 1.m. and 1.25m. The totals were determined by adding the products obtained by multiplying the average per square meter for each station by the number of square meters in it.

The collections were made with two instruments of our own construction. They are the hoe dredge and the sample cutter. The latter is a heavy sheet metal frame 2 dm. by 5 dm. inside measurement. It is open above and below. On the sides and one end it is 12 cm. high with a flange on the upper edge bent outward at right angles. The other end is 6 cm. high with no flange. The flange is merely to stiffen the instrument and to furnish a surface for forcing it into the lake bottom. When forced into the lake bottom, the low end has its upper edge 6 cm. below the soil surface. Into the cut made by this end, the hoe dredge is introduced and drawn to the opposite end of the cutter. When starting the dredge, the handle is at as low an angle to the horizontal as the depth of the water will permit. As the sample is taken it is raised gradually to the vertical. See Plate No. 2.

The hoe dredge is made of 20 or 16 gauge metal shaped like a box with two opposite sides out. It is 2 dm. wide outside measurement and 12 cm. high. In the center of one of the long sides is riveted a base such as is used in fastening iron pipes to floors or other surfaces. A socket with suitable handle screws into this base. On the upper edge of each side a flange is bent outward at right angles. Over this flange a bag is attached with a draw-string.

The sample cutter is ground to a cutting edge with a bevel on the outside while the dredge is ground to a cutting edge with a bevel on the inside.

Samples taken with these two instruments are of rather precise dimensions. These samples can be cut from bottom covered with *Chara* or other prostrate plants. Where the plants are extremely thick, a dredge with a larger opening is required. However, the dimensions given are satisfactory in our lakes.

After a sample is taken it is washed in a net made of number 40 grit gauze. The one used is 40 cm. deep and hung on a triangular frame whose sides measured 30 cm. The washing can be done best by immersing the

lower two-thirds of the bag in the water and alternately raising and lowering the bottom of the bag with the hand. This removes all the fine detritus and marl with minimum injury to the contained organisms. The residue is then placed in buckets and taken to shore for counting. Each form was identified and counted separately. The totals together with depth, temperature, and other physical data are entered on a card.

The weight of the more important organisms were determined. To do this, samples of each organism were counted into a dish containing a small amount of water. After being counted they were placed on a piece of wet bolting silk stretched over the large end of a funnel. By tilting this funnel the excess water was removed. The sample was then placed in a platinum foil dish and weighed on an assay balance sensitive .01 mg. This was recorded as wet weight (W.W.). It was then dried to a constant weight in an electric oven at a temperature of 60°C. The dry weight (D.W.) was then determined. The sample was ashed in an electric furnace at approximately 550°C. The weight of the ash subtracted from the dry weight is regarded as the amount of dry organic matter (D.O.M.) present.

The numbers upon which the average weights of the organisms were determined varied with the size of the organism from four in the case of the odonata to 1,595 in the case of the amphipoda.

Deep Water

The collections in deep water were made on the odd contours from the 3 meter contour on one side of the lake to the three meter contour on the opposite side. Twenty such series were made. The average for all the collections at a given depth was taken as the average for the area enclosed by the adjacent contours. For instance the average of all the collections made at 5 meters was taken as the average for the area between the 4 and 6 meter contours. The number of collections at each depth and the average number of organisms per square meter in each area are given in Table No. 4.

The collections were made with a 6 inch Foerst-Ekman dredge. Two catches were made at each station and averaged. The reduction of the sample with a grit gauze net; the enumeration and record of organisms were made as in the littoral.

This lake, as already indicated, differs from the other Indiana lakes so far examined in the relative slope and area of the S-2 and 2-4 meter regions. In this lake the former has a slope of 2.42 and an area of 568 acres while the 2-4 meter region has a slope of 1.45 and an area of 928 acres. This is due to the larger size of Lake Wawasee (Turkey Lake). The rachine, or wave line, of Muttkowski ('18) is included in the S-2 region.

A study of the material from the deep water indicated that the 2-4 area was distinct from the 4-bottom and hence the results have been grouped in the three levels, S-2, 2-4, and 4-bottom. The areas of these levels are 568, 923, and 1376 acres, respectively.

The S-2 region is exposed to waves and shore currents. Part of it is rather barren sand and marl. Part is covered with chara and at some points it is invaded by the rushes and Potamogeton of the deeper water. In this paper it is designated as the "open littoral."

The 2-4 region is very generally covered with the submerged aquatic phanerogams, most of which are Potamogetons. It is a very productive area of

the lake even when the plants are omitted, although certain forms like the sphaeriidae seem to avoid it. This we call the "weedy littoral."

The area beyond the 4m. contour is called simply "deep."

The Fauna

Quantitative Results

The results are apparent from an inspection of Tables Nos. 4, 6, and 7.

Annelids

These small aquatic worms do not make a large aggregate but they are very generally distributed and form a part of the diet of all small fish. The littoral contains slightly more than the deeper parts of the lake. Table 4 indicates that they are rather irregularly distributed although part of this may be due to errors in counting. They have a habit of balling up in more or less spherical masses so that precise counting is difficult.

Insect Larvae

In the open littoral (S-2m.) the three important groups are the ephemerid (May fly) nymphs, the odonata (dragonfly) nymphs and the chironomid (midge) larvae (sens. lat.) other than *Chironomus tentans*. The wet weight of the chironomids and ephemerids is 28.68 and 28.36 lbs. per acre, respectively. The weight of the odonata nymphs is 6.68 lbs. per acre. The total weight for the insect larvae in this region is 63.72 lbs. per acre.

In the weedy littoral (2m.-4m.) the chironomids are reduced to 11.51 lbs. per A., the ephemerids are negligible (.34) and the odonata are represented by a few damsel fly (anisoptera) nymphs. However, the orl fly (*Sialis*) has become an important element (10.36).

The most important element of the bottom insect fauna of the deep area (4m.-3m.) is the large blood worm, the larva of *chironomus*. The weights are based on a sample of 100 large specimens collected August 7. The totals represent more nearly the maximum than the average for the summer. Based upon this weighing they amount to 326 lbs. per acre in the deep area and about 4½ lbs. for the 2m.-4m. level.

They seem to reach a rather definite maximum at 15 meters where there are 881 per square meter. See Table No. 4. The other chironomids amount to slightly more than half (6.38) those of the weedy littoral. *Sialis* increases to 12.34. The total weight in lbs. per A. of insect larvae in the three depths is 63.72, 26.78, and 348.98, respectively.

The Crustacea

The important bottom crustacea are the crayfish (*Cambarus*) and the amphipods or scuds (*Hyaella* and *Eucrangonyx*). Both of these are important out to about 6 meters and are of especial significance in the open littoral and the weedy littoral.

In the open littoral (S-2) the number of crayfish is greater than our data indicate. The water was clear and some escaped. This was especially true for the larger ones. The crayfish taken were all near the same size, their length being between 2 and 3 inches. It was assumed that they were in their second year although there is no evidence for this assumption other than this uniformity in size.

The total weight of the crayfish in both the open littoral (S-2) and the

weedy littoral (2-4) exceed that of the amphipoda, the weights being 23.41 lbs. per A. and 110.22 lbs. per A., respectively, for the crayfish and 18.05 and 14.25 for the amphipoda. However, this does not represent the true value of the two forms because the amphipoda produce a brood about every twenty-five days while the crayfish breeds once a year.

The Gastropoda (Snails)

On the whole this group is of more importance in the open littoral and weedy littoral than in the deeper water. *Goniobasis*, *Physa*, and *Amnicola* are strictly littoral forms. However, *Planorbis* reaches its maximum at 5m. and *Valvata* at 9 meters.

Goniobasis is the most important member of this group. It forms by weight 97 per cent of all the snails in the open littoral and 74 per cent of all snails in the weedy littoral. The lower per cent of *Goniobasis* in the weedy littoral is due largely to the increase in *Physa* which reaches 90 lbs. per acre in this area.

Amnicola is the most evenly distributed in the inshore areas. It is between 4 and 5 lbs. per acre in both the open and weedy littoral.

Planorbis has a rather general distribution reaching a maximum of 4.69 lbs. per acre in the weedy littoral, its ratios in the three areas being approximately 2-6-3.

The Sphaeriidae

These little bivalves are found everywhere in the lake bottom. *Sphaerium* reaches a very definite maximum at 9 meters. *Pisidium* on the other hand has a decided preference for deep water. It increases directly with the depth until 11 meters is reached, beyond which it remains fairly constant. See Table No. 4.

On account of its greater size, the total weights of *Sphaerium* for all three areas is greater than those of *Pisidium*.

One very interesting fact is shown in Table No. 7. It is that both forms are more numerous in the open littoral and deep water area than in the weedy littoral. In both forms the proportions for the open littoral (S-2), weedy littoral (2-4), and deep littoral (4-22) areas are very close to 6-1-20. The only factor that we have been able to associate with the reduced number in the weedy littoral is the increased number of submerged phanerogams chiefly *Potamogetons*. Why such a relation should exist is not apparent.

Adding the totals in Table No. 7 gives the number of invertebrates on the bottom of Lake Wawasee (Turkey Lake). This number is slightly more than 18 billion.

The wet weight of these obtained by multiplying the total of all forms in lbs. per acre in each area by the number of acres (as indicated in Table No. 6) gives a total wet weight of 2,028,961 lbs. The dry organic matter averages about 9 per cent of this total, which is 182,606 lbs. These numbers are not the absolute facts but they are as close an approximation as is practicable. They are based on two years' collections. Their accuracy can only be increased by increasing the amount of data. The increase in accuracy, however, is not directly proportional to the increase in data. The accuracy of these two years' work would not be doubled by working four years but would require eight years by the well known formula $2 \times 2^2 = 8$. To treble it would require $2 \times 3^2 = 18$ years.

Other work on related lines is regarded as more profitable.

A general discussion of these results, their relation to the problem of the turnover, to fisheries, and to previous work in this field is reserved for the second section of this paper.

Some notion of the work already done on bottom fauna may be obtained by consulting the text and bibliography of Ekman '17, Juday '22, and Adamstone and Harness '23.

Lists of Species:

Specific names have not been used in the body of this paper. They have no particular bearing on the problem in hand and furthermore specific determinations cannot be made in most instances when handling large numbers daily even if the worker were qualified.

Precise determination of species is of great value in the study of distribution; while a mistaken identification only adds to the confusion. The following organisms have been identified or reviewed by the authorities indicated and to whom acknowledgment is hereby made. It is hoped to increase these lists of authoritatively determined material.

Hirudinea (Leeches), identified by Professor J. Percy Moore of the University of Pennsylvania:

Glossiphonia (Helebdella) *stagnalis*
Glossiphonia *nepheloidea*
Glossiphonia *fusca*
Glossiphonia *complanata*
Glossiphonia *heteroclita*
Nephelopsis *obscura*

Hydracarina (mites), identified by Dr. Ruth Marshall, Rockford College:

Name	Depth in Meters	Date	Sta. No.
<i>Limnochares aquaticus</i> (L.), cosmopolitan common..	.5	Aug. 10	87
<i>Limnesia</i> nymph, undetermined	1.	Aug. 7	85
<i>Lebertia porosa</i> Thor, cosmopolitan common.....	1.	Aug. 7	85
<i>Lebertia porosa</i> Thor.....	.5	Aug. 3	81
<i>Lebertia porosa</i> Thor.....	.5	Aug. 7	85
<i>Unionicola crassipes</i> (Müll.), cosmopolitan common..	.5	Aug. 3	81
<i>Hygrobates</i> undeterm. (Nov. spec.?).....	1.	Aug. 7	85
<i>Albia</i> undeterm. (Nov. spec.?), not common.....	.5	Aug. 10	87
<i>Atractides parviscutus</i> Mar., common.....	1.5	Aug. 7	85
<i>Atractides parviscutus</i> Mar.....	.5	Aug. 10	87
<i>Atractides parviscutus</i> Mar.....	1.	Aug. 7	85
<i>Piona reighardi</i> (Wol.), very common.....	1.	Aug. 7	85
<i>Piona reighardi</i> (Wol.).....	.5	Aug. 10	87
<i>Arrhenurus megalurus</i> Mar., very common.....	1.5	Aug. 7	85
<i>Arrhenurus manubriator</i> Mar., common.....	.5	Aug. 3	81
<i>Arrhenurus americanus</i> Mar., very common	.5	Aug. 10	87
<i>Arrhenurus pseudocylindratus</i> Piers., not common..	1.	Aug. 7	85
<i>Arrhenurus</i> fem. unid.....	1.5	Aug. 7	85
<i>Arrhenurus</i> fem. unid.....	1.	Aug. 3	81
<i>Arrhenurus</i> fem. unid.....	1.	Aug. 7	85

Name	Depth in Meters	Date	Sta. No.
Arrhenurus fem. unid.....	.5	Aug. 10	87
Arrhenurus nym. unid.....	.5	Aug. 10	87

Crustacea. Amphipoda (scuds), identified by Mr. C. R. Shoemaker of the
United States National Museum:

Eucrangonyx gracilis (Smith)

Wawasee Lake, Ind. 6-22-1926

Hyalella azteca (Saussure)

7-24-1926

Gastropoda (snails) and *Sphaeriidae* (small bivalves), identified by Mr. Herman
P. Wright, Indiana University:

LYMNAEIDAE

Lymnaea danielsi Baker

PLANORBIDAE

Planorbis antrosus Conrad

Planorbis campanulatus Say

Planorbis exacuus Say

Planorbis exacuus megas Dall

Planorbis parvus Say

Planorbis deflectus Say

PHYSIDAE

Physa integra, var.

Physa sayii, var.

VIVIPARIDAE

Campeloma rufum (Haldeman)

VALVATIDAE

Valvata bicarinata Lea

Valvata bicarinata normalis Walker

AMNICOLIDAE

Amnicola lustrica Pilsbry

Amnicola limosa porata (Say)

Amnicola walkeri Pilsbry

Amnicola pilsbryi Walker

PLEUROCERIDAE

Goniobasis livescens Menke

SPHAERIIDAE

Sphaerium acuminatum Prime

Sphaerium sulcatum Lamarck

Sphaerium rhomboideum Say

Pisidium compressum Prime

Pisidium fallax Sterki

Pisidium variable Prime

Pisidium scutellatum Sterki

Pisidium adamsi Prime
Pisidium medianum Sterki
Pisidium minutum Sterki
Pisidium tenuissimum Sterki
Pisidium concinnulum Sterki
Pisidium vesiculare Sterki
Pisidium superius Sterki
Musculium declive Sterki
Musculium sp.

Formula used in calculating slope:

$$S = \frac{C_1 + C_2}{2} \cdot \frac{I}{A}$$

Where S is the slope between two contours, C_1 and C_2 are the length of the contours, I is the contour interval and A is the area between the contours.

LITERATURE CITED

- Ekman, Sven. 1917. Allgemeine Bemerkungen u. d. Tiefenfauna d. Binnen-seen. Int. Rev. d. ges. Hydrobiol. u. Hydrog. B. VIII, S. 113-124.
 Muttkowski, R. A. 1918. The Fauna of Mendota. Trans. Wis. Acad. Science, Arts, and Letters. Vol. XI, pp. 374-454.
 Juday, C. 1922. Quantitative Studies of the Bottom Fauna in the Deeper Waters of Lake Mendota. Wis. Acad. Science, Arts, and Letters. Vol. XX, pp. 461-493.
 Adamstone, F. B. 1924. The Distribution and Economic Importance of the Bottom Fauna of Lake Nipigon, with an Appendix on the Bottom Fauna of Lake Ontario. Univ. Toronto Studies, Biol. Ser. No. 25, Pub. Ont. Fish. Res. Lab. No. 24, pp 35-100

D	Length of Contour	Area Between Contours sq. m.	% of Total	Slope
S	25,335	2,301,886	19.8	2.42
2	25,335	3,736,669	32.1	1.45
4	30,732	705,719	6.0	9.01
6	31,493	597,176	5.1	11.84
8	30,792	1,005,462	8.6	5.49
10	25,609	1,026,580	8.8	4.00
12	15,512	698,074	6.0	4.46
14	15,658	801,319	6.9	3.22
16	10,121	566,956	4.8	2.63
18	4,817	84,472	.7	8.30
20	2,195	69,202	.5	3.81
22	439	15,253	.1	2.16
		11,608,768		

TABLE NO. 1. Area and slope data for the different levels of the lake.

Depth	Vol. Each Level	% Total	R. T.
S-2.....	21,336,414	27.4	1.83
2-4.....	15,249,929	19.6	1.32
4-6.....	10,852,597	13.9	.93
6-8.....	9,639,360	12.3	.83
8-10.....	8,070,108	10.3	.69
10-12.....	5,462,381	7.0	.47
12-14.....	3,750,775	4.8	.32
14-16.....	2,224,440	2.8	.19
16-18.....	838,191	1.0	.07
18-20.....	248,556	.3	.021
20-22.....	90,372	.1	.007
22.....	7,628		
	77,770,751	99.5	

TABLE NO. 2. Distribution of volumes. The second column is percent of totals and the third is the reduced thickness. The average depth is 6.69 meters or 21 ft. The "reduced thickness" is the depth that level would have if it had an area equal to that of the lake surface and sides vertical. The sum of the R. T. equals the average.

Name of Form	Number per Station		Station Number of Max.	Total
	Avg. Sq. M.	Max. Sq. M.		
Platyhelminthes—				
Turbellaria (flat worms).....	36.7	477	93	76,807,200
Annelida—				
Oligochaeta.....	26.7	145	69	56,073,900
Hirudinea (leeches).....	44.4	457	83	93,097,000
Crustacea—				
Isopoda.....	40.9	2,390	33	278,192,000
Amphipoda (scuds).....	1,463.7	5,505	88	3,063,588,000
Cambarus (crawfish).....	5.2	20	61	11,031,800
Insecta—				
Ephemera.....	152.2	1,390	109	318,971,000
Tricoptera.....	42.2	297	85	89,992,000
Odonata—				
Anisoptera.....	2.0	20	88	2,589,800
Zygoptera.....	1.2	27	83	641,008,000
Coleoptera—				
Imagoes.....	3.0	22	93	6,470,000
Larvae.....	6.1	37	43	12,802,600
Chironomus.....	306.3	1,932	87	641,008,000
Snails—				
Physa.....	29.7	675	85	62,202,000
Goniobasis.....	83.4	427	112	174,601,000
Amnicola.....	29.5	507	63	61,882,000
Planorbis.....	4.5	32	88	9,547,000
Valvata.....	.04	2	59	86,700
Lymnea.....	1.3	3	74	2,727,000
Campeloma.....	.04	2	59	86,700
Lamellabranchiata—				
Pisidium.....	8.7	130	92	51,958,900
Sphaerium.....	33.0	1,375	49	69,175,300
Total.....				5,723,897,900

TABLE NO. 3. In the first column is given the average number per square meter, in the second column the maximum per square meter, in the third column the number of the littoral station where the maximum occurs and in the last column the total number in the littoral region.

All these maxima occurred in the second series except those for the oligochaeta, isopoda and Pisidium.

No. Collections	42	47	46	44	38	37	30	21	24	8	2
Depth	3	5	7	9	11	13	15	17	19	21	23
Turbellaria	14.15	5.70	.93	.48	.56						
Oligochaeta	10.35	5.49	3.29	6.84	13.59	25.00	32.28	14.34	76.76		
Hirudinea	28.18	20.14	6.08	2.93	2.83	.58	.71	1.02			
Sphaerium	2.56	27.93	55.20	116.40	91.74	45.09	28.69	18.44	8.06	5.38	
Pisidium	4.09	7.32	14.97	41.57	117.79	133.77	116.92	115.79	110.29	149.12	
Planorbis	13.83	32.50	30.40	10.27	2.22			1.02			
Goniobasis	71.73	17.39	2.10	.97							
Valvata	9.22	6.86	10.05	14.18	19.25	5.15	3.60		1.79		
Physa	79.92	63.18	11.69	.48	.56		.71				
Amnicola	67.12	53.11	13.09	4.89	1.69	.58	1.45				
Campeloma	1.02		.46								
Amphipoda	1,005.54	255.95	25.98	.48							
Isopoda	127.85	43.74	28.52	1.46	.56						
Cambarus (crawfish)	22.54	13.27	4.67	.97							
Chironomus tentans	7.17	43.96	97.77	300.78	720.92	825.90	881.80	603.58	202.64	306.66	150.04
Other Chironomidae	161.91	59.52	70.17	96.84	122.89	97.71	61.69	106.50	78.01	88.77	118.86
Corethra	1.53	.91	9.35	18.26	62.86	211.71	223.09	189.58	247.84	290.52	225.96
Other diptera	13.17	9.15	5.61	7.33	5.09	2.87	1.43	2.04			
Ephemeridae	75.83	42.12	24.79	7.33	1.69	.58					
Sialis	16.87	6.27	36.72	45.74	29.43	10.46	1.43	1.02			
Damsel fly	4.61	.45									
Tricoptera	17.94	4.10	2.10	.48							

TABLE NO. 4. Distribution with reference to depth of the various "deep" water organisms. Average number per square meter.

Name	Number Weighed	W. W.	D. W.	Ash	D. O. M.
Turbellaria	114	.1876	.0526	.0316	.021
Oligochaeta	454	1.5923			.1854
Isopoda	309	.5946	.2331	.0662	.0427
Amphipoda	1,595	2.5333	.2331	.0662	.1669
Cambarus	6	3.2878	.3433	.1905	.1528
Ephemerida	86	.1906	.0188	.0030	.0158
Odonata	4	.6303	.10353	.02846	.07407
Sialis	4	.276	.0403	.0027	.0376
Chironomus tentans	100	7.0088	.4346	.0651	.3735
Other Chironomidae	531	4.2341	.5004	.1179	.3835
Corethra	274	1.1099	.0779	.0063	.0716
Amnicola	24	.1977	.069	.0421	.0169
Physa	7	.8918	.2102	.1551	.0551
Goniobasis	10	4.7512	2.6368	2.3685	.2683
Valvata	20	.5617	.1879	.1222	.0657
Planorbis	34	1.2932	.4023	.3153	.087
Sphaerium	9	4.0022	1.0742	.9106	.1636
Pisidium	50	.8848	.4159	.2848	.1311

TABLE No. 5. Weight in grams of the various organisms and the number of each weighed. W. W. = Wet Weight. D. W. = Dry Weight. D. O. M. = Dry Organic Matter that is D. W. minus ash.

Description of Areas..... Area in Acres..... Depths.....	Open Littoral 568 S-2 m.	Weedy Littoral 923 2 m.-4 m.	Deep 1,376 4 m.-23 m.
Annelida.....	.59	.49	.47
Isopoda.....	.94	2.17	.16
Amphipoda.....	18.05	14.25	.50
Cambarus.....	23.41	110.22	11.22
Total Crustacea.....	42.40	116.64	12.18
Ephemera.....	28.36	.34	.96
Odonata.....	6.68		
Sialis.....		10.36	12.34
Chironomus tentans.....		4.48	326.24
Other Chironomidae.....	28.68	11.51	6.38
Corethra.....		.09	3.06
Total insect larvae.....	63.72	26.78	348.98
Amnicola.....	4.12	4.93	.70
Physa.....	2.32	90.87	10.74
Goniobasis.....	334.59	304.16	11.03
Planorbis.....	1.41	4.69	2.37
Total gasteropoda (snails).....	342.44	406.96	27.41
Pisidium.....	3.70	.64	12.73
Sphaerium.....	62.74	10.25	235.01
Total Sphaeriidae.....	66.44	10.89	277.74
Total all forms per A.....	515.56	561.76	666.78

TABLE NO. 6. Wet weight (W. W.) of the important organisms in pounds per acre for the three major areas of the lake, the open littoral (S-2m.), the weedy littoral (2m.-4m.) and the deep (4m.-23m.).

Multiplying any of the above numbers by the factor 1.11 will give approximately the number of kilos per hectare.

Area in Acres..... Description..... Depth.....	568 Open Littoral S-2 m.	923 Weedy Littoral 2 m.-4 m.	1,376 Deep 4 m.-23 m.
Turbellaria.....	76,807	52,873	5,635
Oligochaeta.....	56,073	59,354	85,317
Hirudinea.....	93,097	105,299	25,135
Isopoda.....	278,192	477,733	59,740
Amphipoda.....	3,063,588	3,757,370	96,574
Cambarus.....	11,031	84,224	13,127
Ephemera.....	318,971	283,351	54,035
Odonata.....	643,597	17,226	317
Sialis.....		63,037	111,629
Chironomus tentans.....		26,791	2,905,273
Other chironomidae.....	641,008	605,004	499,996
Corethra.....		5,717	441,108
Amnicola.....	61,882	250,805	53,512
Physa.....	62,202	298,634	52,653
Goniobasis.....	174,601	268,031	14,501
Planorbis.....	9,547	51,678	53,694
Valvata.....	86	34,452	51,339
Lymnea.....	2,727		
Campelema.....	86		
Pisidium.....	51,958	15,282	329,858
Sphaerium.....	69,175	9,565	29,858

TABLE NO. 7. Total numbers in thousands in the three areas of the lake.

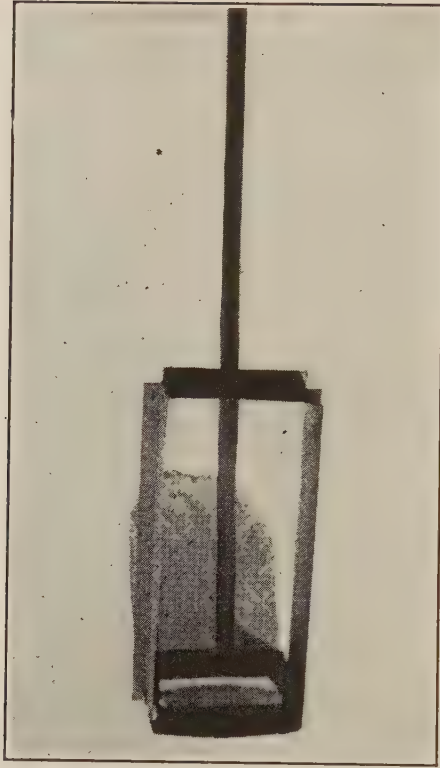


PLATE II. The hoe dredge and the sample cutter with the hoe dredge in place.

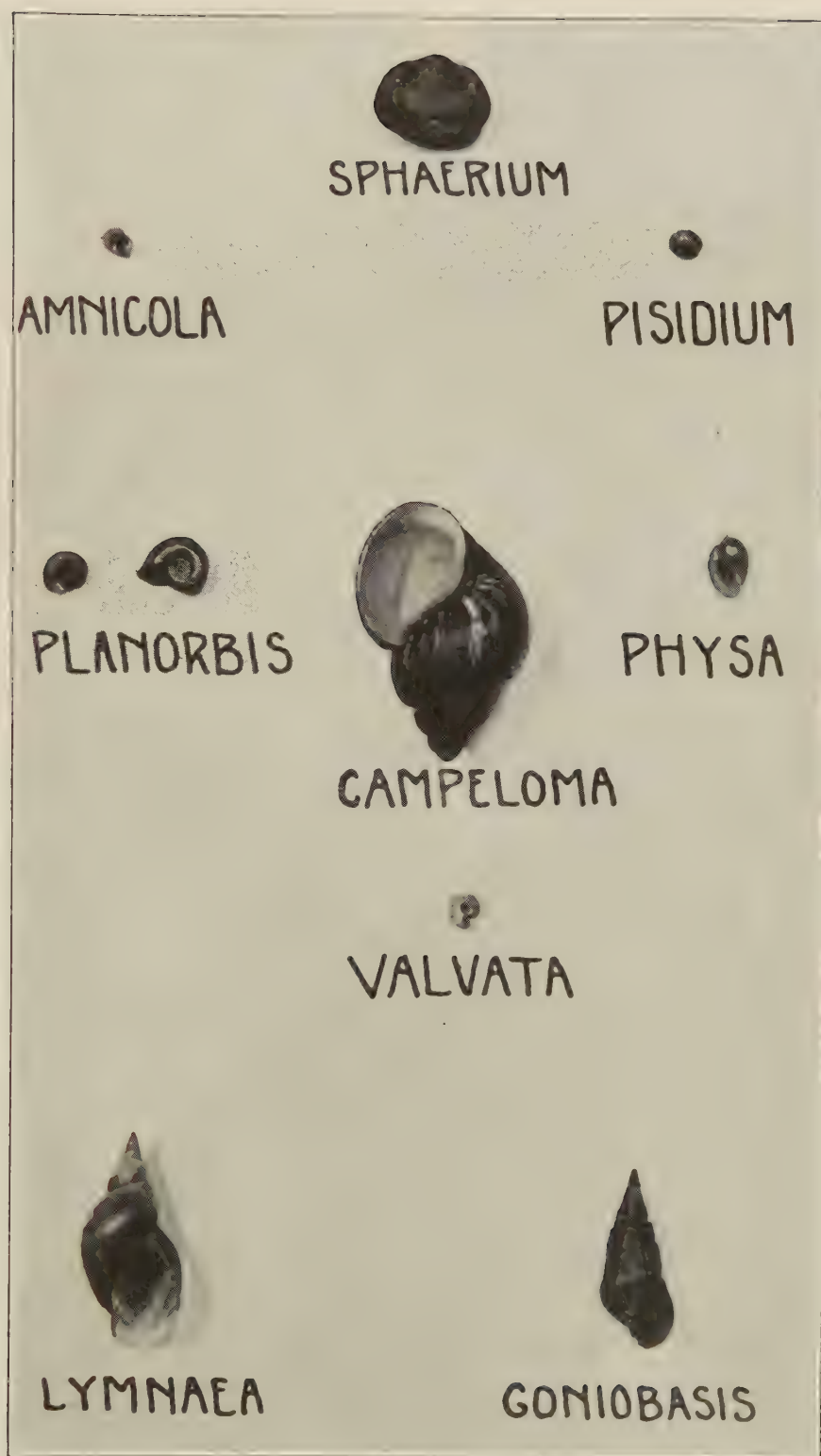


PLATE III. Some of the common genera of littoral gastropods (snails) and the two bivalves Sphaerium and Pisidium.



PLATE IV. Two of the important bottom forms, the large blood worm (*Chironomus tentans*) and the amphipod or scud (*Eucrangonyx*).

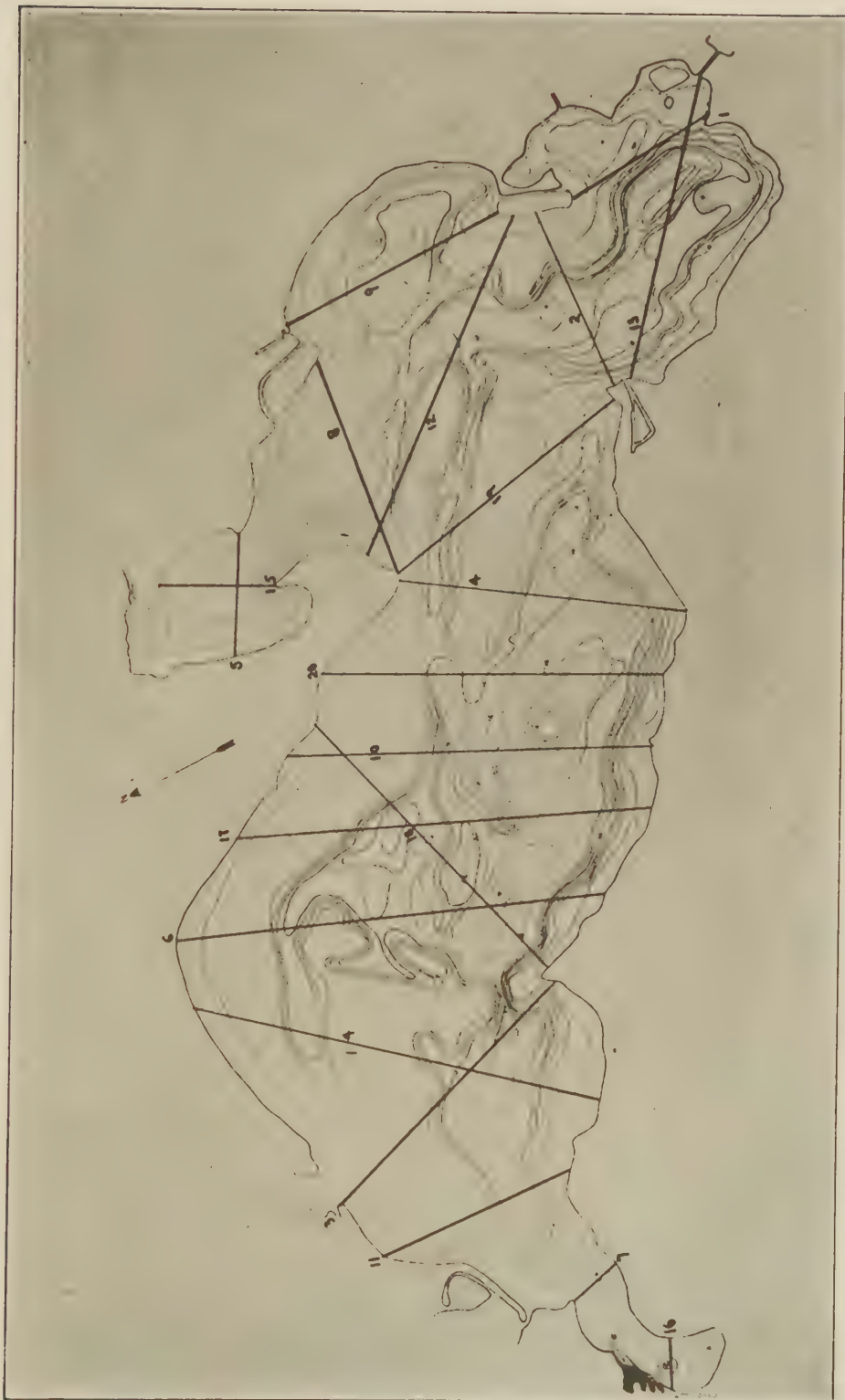


PLATE V. Lake map showing the lines along which the deep water collections were made. The points of intersections of these lines and the contours of 3 meters and deeper are the "deep" water stations.

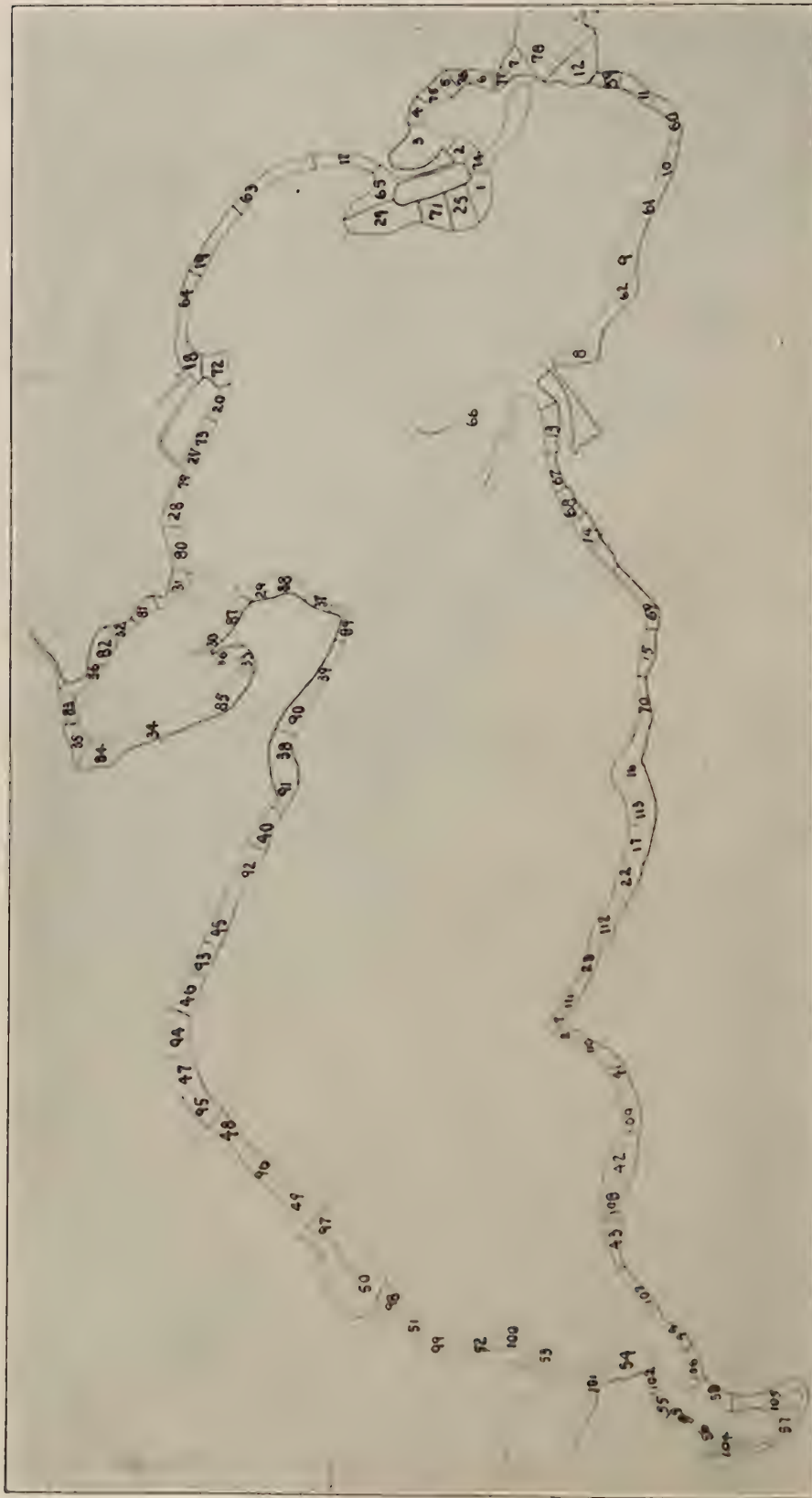


PLATE VI. The litoral stations. This plate in connection with table 7 shows where the maximum of each litoral form occurred.

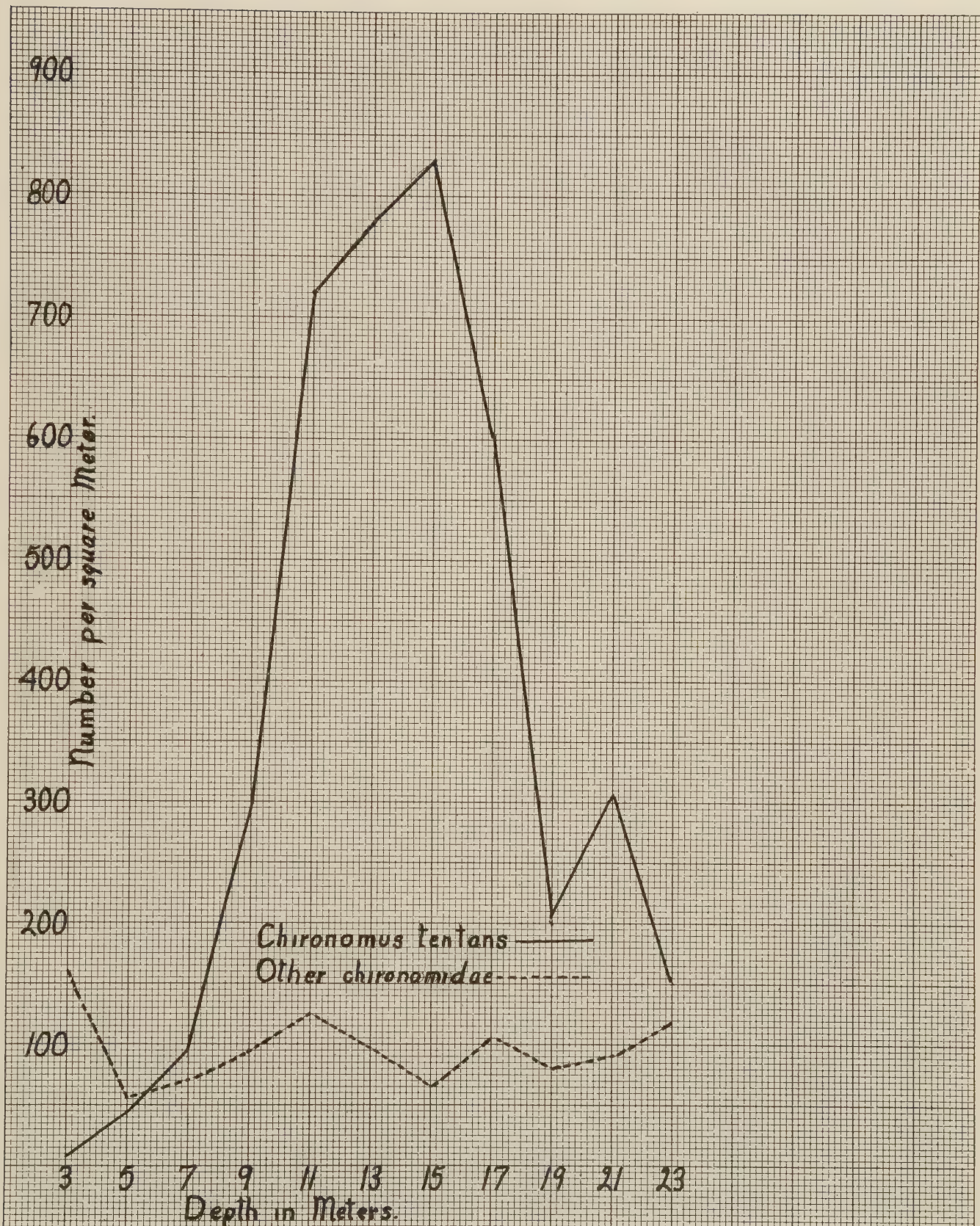


PLATE VII. Depth distribution of *Chironomus tentans* and other Chironomidae.

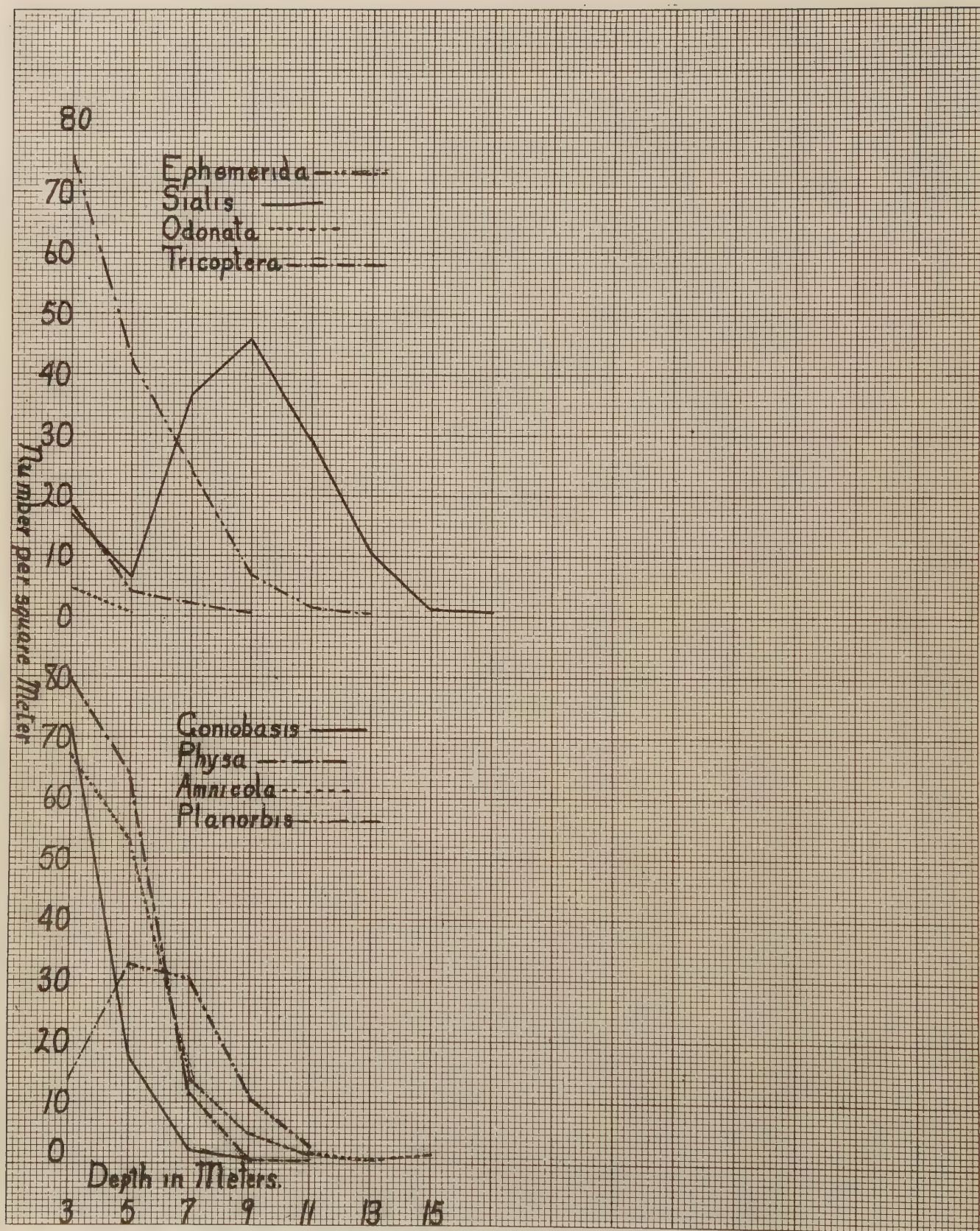


PLATE VIII. Depth distribution. Above four common groups of insect larve. Below: four common genera of snails.

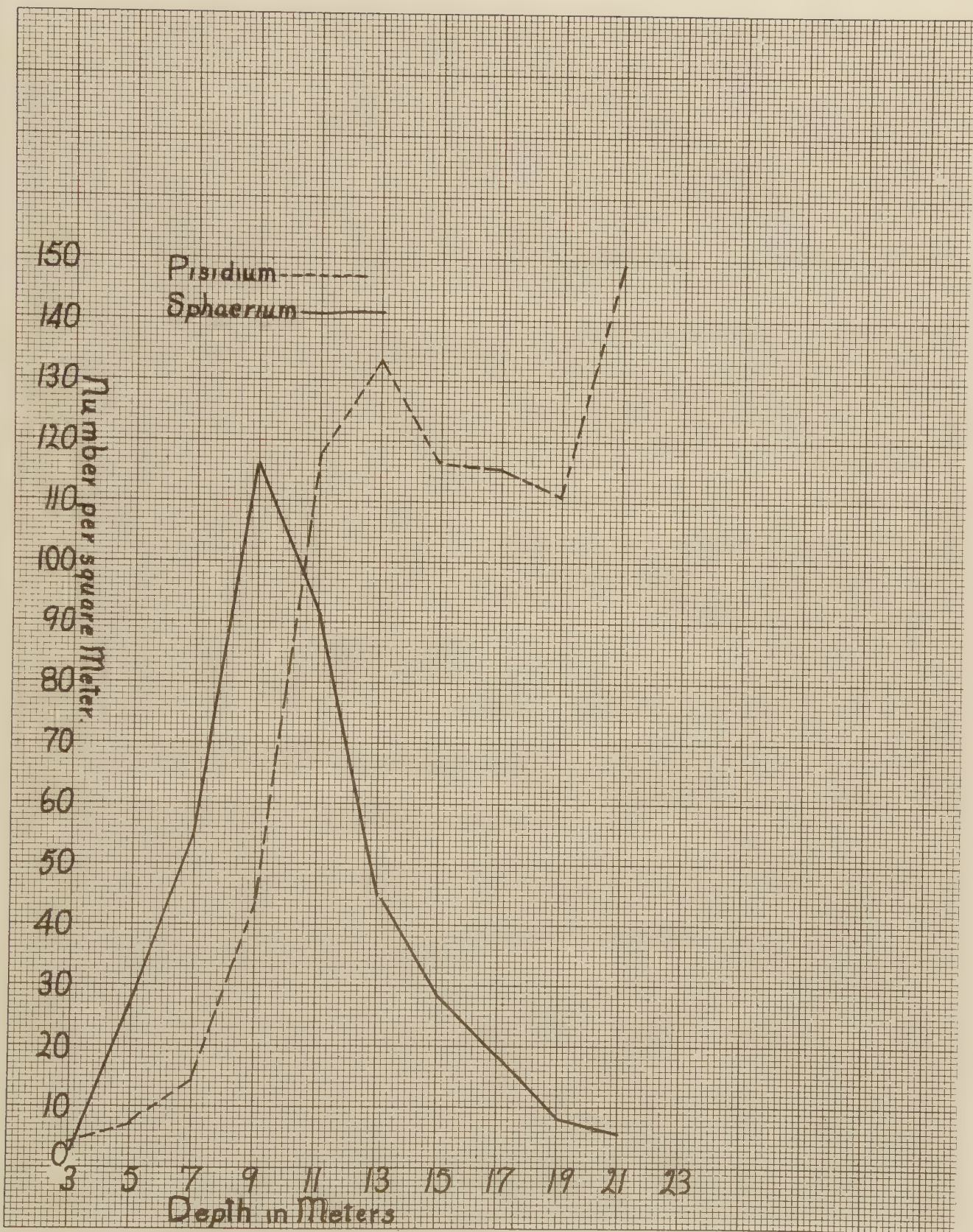


PLATE IX. Depth distribution of the two small bivalves, *Pisidium* and *Sphaerium*.

THE DEPARTMENT OF CONSERVATION

STATE OF INDIANA

INVESTIGATIONS OF INDIANA LAKES

II. The Rate of Growth of Fishes of Indiana

by

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INTRODUCTION

In attempting to arrive at some idea of the productivity of lakes, it is necessary not only to have quantitative data concerning physical and chemical conditions and the amount of food available as plankton and as bottom fauna, but it is also essential to possess information concerning the growth rates of the end products of production, the fishes. It is important to know the extent of the variation of this growth in different lakes, and to detect, if possible, any correlation existing between such variations and influencing environmental factors.

The utter dearth of production statistics stands as a serious obstacle to the investigation of Indiana lake fisheries. Legal bars against the use of nets and seines and against the sale of game fishes preclude the existence of a commercial fishery. Consequently, the fish production of the lakes with its annual and seasonal variations is largely a matter of surmise. There exist few authentic data upon which to base an estimate.

On the basis of quantitative faunistic studies, we are justified in expecting Indiana lakes to be excelled by none in the production of fishes. Yet there is a constantly increasing cry that "fishing is not what it used to be." Each year more and more people leave the state to fish in lakes which are very probably biologically poorer than our own. In the face of this situation, we are quite without means of determining the degree of the decadence of our fishery, or of judging of its causes; whether it be over fishing, the abundance of predatory enemies, food competitors, or some undetermined and unsuspected factors.

Further, it is unfortunate that, with the exception of one brief paper on the subject (Bolen, 1925), no previous studies of growth rate of fishes in any of the lakes here considered have been made. Had such researches been carried on prior to and during the time of the rapid development of lake resorts with its accompanying increased toll on the fish population, it is highly probable that extremely interesting and instructive results would have been obtained. If increased fishing (and the resultant depletion of the stock) has brought about a change in the growth rate as Strodman and Langhammer (1925) found in the Baltic plaice, we have no evidence for it.

It is the purpose of this investigation to make an estimate of the growth rate in different lakes for the species studied. The extent of size variation of single age groups from lake to lake and at different times in the same lake will be noted. The increase from one year group to another within the same lake will be indicated. The relationship between weight and length in different collections is determined with a view towards ascertaining the condition of the different groups of specimens. The possible role of food as a factor determining growth and condition will be briefly considered.

ACKNOWLEDGMENTS

I wish to acknowledge my great indebtedness to Dr. Will Scott, Professor of Zoology at Indiana University and Director of the Biological Station, for his valuable advice and supervision during the execution of this work. I am further indebted to Dr. Scott for the scale photographs appearing in this paper.

The Division of Fish and Game of the Department of Conservation, State of Indiana, rendered possible the collection of the data by financing the field work and by furnishing permits for the use of seines and nets.

I wish to thank the persons who, at different times, assisted me in the work of collecting. Mr. John Fleming of the Wawasee Hatcheries aided greatly in the collecting of material in that region. During the summer of 1929, various students from the Biological Station worked with me on collecting trips.

The manuscript has been read and criticized by Dr. Scott and other members of the department.

MATERIAL

The present study is based upon material collected from twenty lakes in Kosciusko and Noble Counties. These lakes are distributed in three drainage areas¹ as follows:

Elkhart Drainage Area

Lake: Syracuse
Wawasee (Turkey)
Papakeechee
Indian Village
Duley
Rider
Gordy
Hyndman
Dewart

Tippecanoe Drainage Area

Lake: Spear
Ridinger
Dan Kuhn (East)
Big Barbee (Hammon)
Little Barbee
Tippecanoe
Little Chapman (Little Eagle)
Pike
Little Pike
Center
Winona (Eagle)

Eel Drainage Area

Lake: Silver

The total number of specimens studied was 1,955.

¹ Hydrographic maps of Dan Kuhn, Chapman, Big Barbee, Ridinger, and Silver Lakes are available in a report by Scott (1916). Maps of Indian Village, Duley, and Gordy Lakes are soon to be published by Dr. Will Scott. Maps of Wawasee and Tippecanoe have been made by the Indiana Department of Conservation.

The following species are represented in the collections:

Family Centrarchidae

Blue Gill	<i>Helioperca incisor</i> (Cuvier and Valenciennes)
Black Crappie	<i>Pomoxis sparoides</i> (Lacépède)
Rock Bass	<i>Ambloplites rupestris</i> (Rafinesque)
Small Mouth Black Bass	<i>Micropterus dolomieu</i> (Lacépède)
Large Mouth Black Bass	<i>Aplites salmoides</i> (Lacépède)
Longeared Sunfish	<i>Xenotis megalotis</i> (Rafinesque)

Family Percidae

Ringed Perch	<i>Perca flavescens</i> (Mitchill)
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Family Coregonidae

Cisco	<i>Leucichthys artedi</i> (Le Sueur)
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Family Esocidae

Pickerel	<i>Esox lucius</i> L.
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Family Moronidae

Silver Bass	<i>Lepibema chrysops</i> (Rafinesque)
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The material for this study was, for the most part, collected during the summers 1926 to 1929. Small collections of perch from Lake Wawasee and of blue gills and cisco from Gordy and Indian Village Lakes were made in the late autumn and early winter of 1928. Collection of blue gills and crappies from Indian Village and Duley Lakes, and of a few bass from Wawasee were made in the latter part of April, 1929. In the first three of the summers mentioned, the collections were somewhat incidental to quantitative bottom fauna researches then in progress at Lakes Wawasee and Tippecanoe. The entire summer of 1929 was spent collecting examples from the older year classes in different lakes.

Various methods were employed in securing samples. Many specimens were kindly furnished by fishermen who had taken them by rod and line. Most of the younger year groups (perch, blue gills, black bass, and rock bass) were taken by a 30 foot small meshed seine. All the ciscoes and the older year groups of the other species collected in 1929 were taken by a gill net of 1½ inches mesh. Selection, especially by the gill net and to a lesser degree by seine and by hook and line doubtless took place.

In the case of specimens taken by hook and line, difficulty in taking the hook is certainly a selective factor among the smaller fish.

Larger fish escape a seine more readily than do smaller. This factor is negligible, particularly due to the great degree of uniformity of size in the early year classes combined with the great scarcity of older fish in seine catches. Variation of distribution as to depth, correlated with the size of the fish, is probably a greater factor for selection. It is a matter of common observation that fishes tend to distribute themselves from the shallow littoral region to the deeper waters according to the size of the individual. A seine operating in shallow water only could easily miss the larger specimens of a year class. Here the uniformity of size within the first few year groups tends to minimize selection.

The specimens were weighed and measured, and scale samples taken, within a few minutes or at most within a few hours after capture. Length was measured with wooden calipers from the tip of the snout to the edge of the last scales. Readings were made to the nearest one-sixteenth of an inch, and later converted to the nearest millimeter. Weights were taken with Cenco spring balances of 250 and 2,000 grams capacity. The former were graduated in divisions of 10 grams and estimated to the nearest gram; the latter were graduated in divisions of twenty-five grams and estimated to the nearest five grams. A few of the larger specimens (pike, bass) were weighed to the nearest ounce on grocery scales.

Scale samples were taken from the anterior region near the lateral line. They were stored in small envelopes on which were recorded at the same time the details of name, length, weight, and place and time of capture.

Table LXXXI gives the details of numbers of each species collected in the different lakes.

In securing the material for this growth study, it was necessary to effect a three-way compromise based on desire, expediency, and availability, with the latter factor usually dominant. The wish to secure data from as many representative lakes as possible prevented the taking of large samples from any one lake. In several lakes, the results of fishing proved so meager that any attempt at securing a satisfactory sample would be impractical because of the great amount of time required. The gill net used in the summer of 1929 was 160 yards long and had a depth of 12 feet. Yet quite frequently a set of five or six hours netted a catch of less than twenty specimens. As an illustration of the scantiness of the catches, it may be cited that Pike Lake was visited four days, Spear Lake three days, Big Barbee, Little Barbee, and Silver Lakes two days, and Kuhn Lake one day with the results as indicated in the table. The smallness of the catches seems significant in view of the general complaints concerning the decline of fishing and the depletion of the stock.

With the younger year groups, it was usually sufficient to study the scales dry under the microscope. The scales of the older fish were soaked in water, cleaned by rubbing between the folds of a rough linen towel, scrubbed with a small tooth brush, and returned to a watch crystal of water for examination.

THE DETERMINATION OF AGE

The determination of age depends upon the interpretation of structures appearing in the superficial sculpturing of the scale. The annulus or year mark is in the nature of a line of discontinuity dividing two fields of growth. Towards the close of the summer the fish experiences a retardation of growth. During the cold months growth must be very slow, and observations of several investigators indicate that in many instances, at least, it ceases entirely. With the resumption of rapid growth in the spring, the sculpturing of the new area of the scale is laid down with no particular reference to that of the old. A distinct line of demarcation between the two fields results. The annulus does not become definitely apparent until new growth has appeared. If scales be examined from fish taken in the winter or early spring, there will be observed about the periphery the broad band of growth of the preceding season, but no year mark is to be seen.

Several characteristic structures aid in the detection and recognition of the annulus. The first circuli of the new growth of the spring tend to be complete in the postero-lateral region of the scale, whereas the later circuli of the preceding season end at the edge of the scale in this same region. The new lines of growth here meet the older at an angle, producing "cutting over." The degree of prominence of this feature depends largely upon the form of the scale, and becomes less noticeable where there is slight imbrication and the scale retains a rounded form. The annulus is further characterized by the tendency of the circuli to be faint, distorted, and fragmented. A third aid in the detection of the annulus depends on the approximation of the circuli which accompanies the slowing down of growth. The degree of approximation of the circuli is quite variable. In some instances it is hardly noticeable, while in others it may be so great as to cause the appearance of distinct dark bands. These bands are more prominent in the later than in the earlier years of life. Such dark bands are not to be considered as infallible indicators of annuli, for they are of common appearance within summer growth areas. In general, age readings are independent of the shading of the scale. In the region of the ctenii may be observed distinct successive belts, resulting from the different amounts of time the ctenii of succeeding growth zones have been subjected to wear.

Scales are often lost accidentally and regenerated. These regenerated scales have a characteristic appearance which makes them easily identified. The replaced portion is thinner than the original scale, and lacks its typical sculpturing. The center consists of a large plate with no circuli. Towards the outer part of the regenerated portion appear circuli irregularly and widely spaced. Growth occurring beyond the regenerated portion is normal. Such scales are obviously worthless for age determination.

Occasionally scales are loosened and displaced in the pocket, but not lost. In further growth the normal form and position of the scale are reestablished, and the displaced portion appears in the role of an abnormal center.

Frequently injuries involve the destruction of only a part of the scale. Such injuries are repaired, but they disturb the regular sculpturing of the scale.

By comparing partially or wholly regenerated scales with normal scales taken from the same individual, it is possible to determine at what period in the fish's life a particular injury occurred.

The chief difficulties in the use of scales for age determination center about the matter of false rings or accessory annuli. These checks appearing within the growth areas would, if interpreted as true annuli, lead to erroneous age determinations. They may usually be detected by their peculiar appearance or by their position with respect to the true annuli. Some false rings appear consistently in all scales and seem to be the result of conditions affecting the entire fish. Others lack such general distribution and seem to result from irregularities of growth within individual scales.

In many instances accessory growth checks are detectable by being less definite than the true year mark. Cutting over is less pronounced, and the degree of definiteness varies in different parts of the scale, the check being quite prominent in some regions and almost indistinguishable in others. The examination of a considerable number of scales is helpful in determining the validity of a questionable year mark. It is a matter of importance that

scales bearing accessory annuli often present a characteristic confused appearance which puts the investigator on his guard. In a small percentage of cases the sculpturing of the scale may be so confused as to render the scale quite useless for age determination.

Prior to Hoffbauer's (1898) paper lepidologists had confined their attention to the study of the intimate structure and development of scales.¹ Although the use of scales for age determination had been suggested, nothing of a definite nature had been accomplished in that direction. A method of ready age determination filled a deeply felt need of many fisheries investigators. Consequently it became at once the subject of investigation for many workers. A detailed and critical analysis of its basic assumptions followed. Its validity was tested and checked from different angles. Today the literature on the subject is voluminous.

It lies neither within the scope nor the purpose of this paper to enter into an extensive historical and critical survey of the literature on fish scales. Such reviews have appeared from time to time, and are easily available.² For the purpose of this investigation it is assumed that the validity of the annulus as a true year mark has been sufficiently well established. With the problems pertaining to the use of scales for the calculation of growth, the present study is not concerned.

FOOD AND GROWTH

The task of correlating growth with food conditions is one beset with difficulties. Waiving such factors as chemical condition, average water temperature, the presence of races, etc., let us outline briefly the data concerning which we need information in order to proceed towards a solution:

- (1) Available food supply.
- (2) Food habits of species considered.
 - (a) Variation with increased size.
 - (b) Seasonal variation.
 - (c) Amount of food selection and degree of flexibility of diet.
- (3) Density of population.
- (4) Competitors for food.

1. *Available Food Supply.*

The accumulation of data on the amount of food available is a slow and laborious process. Studies must be made concerning both bottom and plankton forms. The values of estimates are greatly enhanced if they are so distributed as to give ideas of the seasonal variation and the variation from year to year. In addition to an estimate of the "standing crop" or food present at a given time, it is well to have some notion of the "turnover" or actual consumption of food. The importance of the problem of production has led to the recognition of the special field of production biology. Calculations of production must be based on a knowledge of standing crops at

¹ Baudelot (1873) in addition to his own observations on the structure and development of the scales gives an historical review of the work done up to that date. Thomson (1904) also gives a review of the nineteenth century literature bearing on the subject.

² For historical summaries and discussion of the scale method, consult Dahl (1909), Taylor (1914), Lee (1920), Creaser (1926), and Van Oosten (1928). Special bibliographies on the subject have been published by Hutton (1921) and Mohr (1927). Graham (1928) gives a survey of the literature which includes abstracts of about seventy papers.

successive periods of time and of the life histories (reproduction, growth rate) of the food forms considered.

The investigators, Peterson, Jensen, Blegvad, and others working from the Danish Biological Station, have studied the problem of production in considerable detail. Their estimates based both on calculation and direct experimentation indicate that the actual production of an area during a given year may at times be greatly in excess of the standing crop at any particular time. Considerable variation from year to year was also noted. It is to be noted further that the absolute density of population may be of importance, for a fish forced to glean a living from a sparsely populated area would be handicapped even in the absence of competitors.

2. *Food Habits of Species Considered.*

(a) That the feeding habits of fishes must change with continued growth is too obvious to require discussion. With increasing size the individual becomes capable of seizing and devouring larger and larger prey, while the forms which formerly constituted his staple articles of diet become too insignificant to warrant the exertion and attention required for their capture. If there is present an adequate supply of all types of food, no inconvenience will result from the change of habit. If, on the other hand the region inhabited is plentifully supplied with food adapted to small fish, but poorly supplied with food for adults, or vice versa, and if migration to more desirable feeding grounds is not feasible by reason of distance or natural barrier, the nature of growth is likely to be affected correspondingly. Borley (1912), in his studies of the condition of plaice in the North Sea, detects regions which are favorable for the growth of the young, but not of the adult. He explains the better growth of plaice on the Dogger Bank on the basis of the excellent supply of food for *adults* there present.

(b) The problem of seasonal variations in feeding habits is connected with food forms having a brief life history. Different food forms show great variation as to numbers at different times of the year. There are definite times of scarcity and abundance. A particular region may at one season be a very rich feeding ground, and at another much less favorable. There may also be a seasonal variation in diet brought about through voluntary selection on the part of the fish. Todd (1915) finds the plaice feeding predominantly on Polychaets in the winter and on Mollusca in the summer. He suggests that the crowded condition of the viscera due to the swelling of the sexual organs might cause particles of shells to be a source of "considerable danger or discomfort." Hardy (1924) suggests that the marked seasonal changes of diet in the herring and mackerel may be due to the need of nourishment for the ripening gonads.

(c) To say that a given form is an element of the food of a certain fish may imply that the fish consumes this form by predilection or through force of necessity. In the presence of a great abundance and variety of food, a fish may well afford to exercise choice and select that which seems most suitable. But what is the condition in the case of a scanty or monotonous food supply? Will the species concerned fail to inhabit such a locality altogether, or will it adapt itself to the adverse conditions of living?

Hertling (1928), in a detailed study of the stomach contents of the plaice, dab, and flounder, correlated with bottom fauna data, found a distinct variation in the food of the three species, correlated definitely with structure

and habit. Such were the conditions where a considerable variety of food was present. Yet in the Gotlandmulde inhabited by an animal community devoid of molluscs (Tiefengemeinschaft), the flat fishes seemed to have been able to accommodate themselves to a diet consisting exclusively of annelids and crustaceans.

Jensen (1919), in a similar investigation, concludes that "it is mainly the same species, which are found in stomach content and in bottom." There was, however, some degree of selection noticed.

3. *Amount of Food per Individual.*

It is not so important to know the actual amount of food present as the actual amount per individual. The amount of food per individual is a factor mutually interactive with the density of population. A region which might naturally constitute an excellent feeding ground may be held in a statement of impoverishment by a too dense population. Further, the value per individual of any definite amount of food is dependent upon the number of feeders.

Precise and definite data as to density of fish population are, of course, difficult to obtain. It is an easier task to relegate comparable areas to such categories as very dense, dense, . . . to very sparse. Such a classification, while certainly lacking in mathematical definiteness, suffices in most instances for purposes of comparison. Data concerning the relative abundance of fishes are mostly obtained through experimental catches and from fisheries statistics.

There are numerous instances cited in the literature of the relationship between density of population and growth rate.

It was early observed by Danish fishermen in the Limfjord that plaice were plentiful but undersized in the Thybown Channel and adjacent parts of the North Sea and Nisum Broad, while they were scarce but of good growth in the inner broads. On the basis of these observations, it was decided to try the effect of transplantation of the small fish to the inner parts of the Limfjord. The first transplantation was made in the spring and summer of 1892. The good results obtained led to a continuation of the work up to the present time. (Due to war conditions, no fish were transplanted in 1917.)

The increased rate of growth resulting from the transfer to regions having more plentiful food made the experiments quite profitable. Although approximately three-fourths of the fish are retaken within the same calendar year of liberation, the yield amounted to 3.5 tons per ton planted for the years 1901-07. Recent years have showed a tendency for the yield to decrease.

Within recent years the flat fish fishery of the Western Baltic has suffered severe depletion. Strodtmann and Langhammer (1925) have noted that there has been at the same time an increase of growth rate. The better growth they attribute to more favorable food conditions. Hertling's study of stomach contents, correlated with bottom sample statistics, seems to support their contention.

Huitfeldt-Kaas (1927) assigns as chief cause for variation in weight and size in different localities " . . . the varying access to the food on the part of the fish." He regards the "dwarf races" as starvation forms. In an earlier paper by the same author,¹ the relationship between overpopulation

¹ This paper is summarized by Rugde in *The Salmon and Trout Magazine*, No. 34, December, 1923.

and starvation forms is discussed. It is a custom among the Norwegian farmers to "keep the trout under discipline." If the fish in a particular lake begin to appear undersized and emaciated, they proceed to remedy the condition through more intensive fishing. If the trout become scarce, restrictions are laid upon fishing. Such control is simple and, on the whole, quite effective in the regions where the trout is the only species of fish. Where there are numerous species of fish, control becomes quite difficult.

After the trout, which was introduced into New Zealand, became numerous, that country was confronted with a pressing problem of overpopulation. A review of Tillyards' paper on the subject appears in the *Salmon and Trout Magazine*. The trout, finding themselves in an environment rich in natural food, fed voraciously, and increased prolifically. Their growth was rapid, and they attained unusual sizes. The native stock of insect forms was unable to maintain itself against such incursions with the result that there in time came to be a plentiful supply of trout and a very scant amount of food. The trout began to show poor condition, and to be subject to parasites. As a remedy, Dr. Tillyard recommends the relaxation of legal restraints to the taking of trout and the confining of spawning to certain selected streams (to be changed from year to year).

Pirognikoff (1927) describes another instance of the relationship between density of population and rate of growth. By comparing his own data on the growth of the dace (*Rutilus rutilus lacustris* Pallas) in Lake Chani with earlier data, he has detected a distinct decline in the rate of growth since 1918. The falling off in growth is considered the result of the decline of the fishery. Intensifying of the fishery is suggested as a remedy.

4. *Competitors for Food.*

Where several species live in a state of common competition for food, the matter of relationship between population and food supply becomes quite complex. It is now important to have knowledge of the details of the feeding habits and abundance of several forms. The "degree of competition" should be known, for it is not likely that several species will have identical tastes and feeding habits.

An interesting study of the feeding relationships of different species is given by Blegvad (1927). The cod fisheries of the Limfjord are subject to marked periodic variations. The viviparous blenny, *Zoarces*, and the gobies upon which the cod feeds voraciously show an abundance approximately in inverse ratio to that of the last named fish. Since *Zoarces* and the gobies are food competitors of the plaice, it is to be expected that in their periods of abundance the amount of available plaice food will be lowered. Such seems to be the general trend. Blegvad points out that, in the years 1924-27, there has been an increasingly poor catch of cod. At the same time, the number of *Zoarces* has increased enormously, while the plaice food per unit area of bottom has diminished notably.

AVERAGE LENGTH AND WEIGHTS IN THE VARIOUS COLLECTIONS

In the following sections will be presented the data from the different collections in the various lakes. There will be presented for each species in each collection the number of individuals in each year class with the average values for weight in grams and length in centimeters. This material is given for the

greater part in tabular form. The tables are accompanied by statements of the method of collection and by the discussion of significant points in the data.

The ages, O, I, II, ——— refer to the number of winters through which the fish have lived. Thus, a fish in the summer in which it has been hatched belongs to the O group, for it has passed no winters and shows no annuli. In the second summer after its hatching, it has passed one winter and accordingly belongs to the I group; in its third summer it belongs to the II group; in the fourth to the III group ———. The various groups are designated as the first summer, one year, two years, ——— classes. An explanation of the terminology used is necessary since some workers have used the numbers I, II, III, ——— to designate the numbers of summers passed by the fish. Under this system, for example, a fish in its second summer belongs to the II group.

While the latter system would be the more suitable in the case of such forms as the cisco which is ordinarily taken at the close of a growing season, the method of designating age by the number of winters is employed throughout this paper as being more descriptive for the material at hand, for few of the specimens studied here were taken either near the beginning or the end of a growing season.

SYRACUSE

Collections were made July 3, 1926, and July 7 and 8, 1927. The 1926 collection, which was furnished by fishermen at the lake, consisted of 22 blue gills and 2 perch. The 1927 collection was taken by a small mesh 30 foot seine. It contained 19 perch, 15 large mouth black bass, 13 rock bass, 10 longeared sunfish, and 7 blue gills—all belonging to the early year groups.

Two III group perch taken in 1926 had an average weight of 79 grams, and an average length of 14.7 cm.

TABLE I.
Syracuse Blue Gills 7/3/1926

Age	Number	Weight	Length
II	19	64	11.2
III	1	180	17.3
IV	1	173	17.1
V	1	210	17.6

TABLE II.
Syracuse Perch 7/7 and 8/1927

Age	Number	Weight	Length
O	3	..	4.2
I	12	12	9.6
II	4	21	11.1

TABLE III.
Syracuse Large Mouth Black Bass

Age	Number	Weight	Length
O	1	..	3.7
I	13	14	9.5
II	1	55	14.0

TABLE IV.
Syracuse Rock Bass

Age	Number	Weight	Length
I	4	6	5.9
II	8	33	10.0
III	1	72	12.9

TABLE V.
Syracuse Longeared Sunfish

Age	Number	Weight	Length
I	1	8	6.4
II	6	26	9.2
III	1	35	10.0
IV	1	50	11.1
V	1	63	12.4

TABLE VI.
Syracuse Blue Gill

Age	Number	Weight	Length
I	3		5.1
II	4	26	9.7

WAWASEE (TURKEY LAKE)

Collections were taken from Wawasee each year from 1926 to 1929. The totals include 635 yellow perch, 157 blue gills, 56 rock bass, 53 large mouth black bass, 13 black crappies, 10 small mouth bass, 5 pickerel, and 3 longeared sunfish—in all, 932 specimens.

YELLOW PERCH

The perch from the 1926 collections were furnished by fishermen, and were taken by hook and line. Table VII summarizes the data on these specimens. Since the times of catching were scattered through the latter part of July and the early part of August, all collections are considered together.

TABLE VII.
Wawasee Yellow Perch—1926

Age	Number of Specimens	Average Length	Increase	Per Cent Increase	Average Weight	Increase	Per Cent Increase
I	5	9.4			10.8		
II	25	13.7	4.3	46	43.6	32.8	304
III	27	16.6	2.9	21	75.6	32.0	73
IV	9	19.3	2.7	16	137.3	61.7	82
V	3	22.0	2.7	14	179.7	42.4	31

TABLE VIII.
Wawasee Yellow Perch—1927

Age	Number of Specimens	Average Length	Increase	Per Cent Increase	Average Weight	Increase	Per Cent Increase
0	9	3.4					
I	216	8.8	5.4	162	10.5		
II	70	13.5	4.8	54	41.9	31.4	299
III	2	16.8	3.2	24	94.5	52.6	125

The data indicate the greatest increase in length in the first three years of life. The weight increase mounts consistently, reaching a maximum from the third to the fourth year. Growing with respect to both length and weight appears to be slowing down from the fourth to the fifth year. Attention should be given to the column showing percentages of increase. Each percentage tabulated is a comparison between the increase for the year and the weight or length for the preceding year. The greatest actual increase and the greatest percentage increase in length occur from the first to the second year.

The averages for 1927, Table VIII, compare well with those of 1926. The differences are no greater than might be expected to result from smallness of samples, differences in time and method of collection, and from experimental error in measurement.

All but three of the perch collected in 1927 were taken by seine at the south end of Morrison's Island. The dates of collection were July 7, 14, 28. The samples were sufficiently large that they should show an increase in size

between the succeeding times of collecting. Such increase is clearly indicated in the data of the following tables.

TABLE IX.
Wawasee One Year Perch—1927

Date of Collection	Number of Specimens	Length	Increase
7- 7-1927	27	8.31	
7-14-1927	153	8.78	.47
7-28-1927	36	9.16	.38

TABLE X.
Wawasee Two Year Perch—1927

Date of Collection	Number of Specimens	Length	Increase
7- 7-1927	11	12.99	
7-14-1927	38	13.44	.45
7-28-1928	18	13.84	.40

Collections were made in 1928 on June 19, 20, 28, and 30, August 14, and November 10 and 11. The last of these collections was made by means of a gill net at the south-eastern extremity of the lake. The others were made by seine at the southern end of Morrison's Island, and are strictly comparable to the collections of 1927.

TABLE XI.
Wawasee Perch—1928

Age	Number of Specimens	Average Length	Increase	Per Cent Increase	Average Weight	Increase	Per Cent Increase
0	10	4.4					
I	77	8.1	.37	84	8		
II	106	12.0	.39	48	28	20	250
III	3	16.8	4.8	40	75	47	168
IV	4	20.3	3.5	21	147	72	96

TABLE XII.
Wawasee One Year Perch—1928

Date of Collection	Number of Specimens	Length	Increase
6-19, 20	21	7.5	
6-28	5	7.7	.3
6-30	25	7.9	.2
8-14	26	9.0	1.1

TABLE XIII.
Wawasee Two Year Perch—1928

Date of Collection	Number of Specimens	Length	Increase
6-19, 20	18	11.7	
6-28	14	12.1	.4
6-30	74	12.0	— .1
10-10, 11	7	16.4	

The total length increase indicated from June 19 to August 14 is 1.6 centimeters.

The growth from June 19 to June 30 was between .3 and .4 centimeters. The large average for the November sample was probably the result of selection by the gill net.

A single collection was made in 1929 on July 1.

TABLE XIV.
Wawasee Perch—7/1/29

Age	Number	Weight	Length
I	38	7.1	8.1
II	18	32	13.5
III	1	52	16.4

The length increase from the I class to the II class was 4.4; the weight increase 25 grams.

For a summary of all perch collections on Wawasee consult Table LXXVIII. It will be seen that on the whole there is good agreement between the averages for the different years, particularly in the early year groups.

BLUE GILLS

During July and August, 1926, measurements and scale samples were taken from 111 blue gills furnished by fishermen at the lake. Collections of later seasons were small and scattered.

TABLE XV.
Wawasee Blue Gills—1926

Age	Number of Specimens	Length	Increase	Per Cent Increase	Weight	Increase	Per Cent Increase
II	77	11.4			49		
III	18	15.5	4.1	36	132	83	169
IV	14	18.4	2.9	19	210	78	60
V	7	19.3	.9	5	246	36	17
VI	1	21.0	1.7	8	325	79	32

The greatest actual and percentual increase in the above collection was from the II to the III class. There were no data on the O and I year classes. The data for later collections follow:

TABLE XVI.
Wawasee Blue Gills—July, 1927

Age	Number	Weight	Length
I	14		5.3
II	7	29	9.8
III	2	250	20.2

TABLE XVII.
Wawasee Blue Gills—6/30/1928

Age	Number	Weight	Length
III	1	123	14.1
IV	2	183	17.2
V	6	244	18.2
VI	1	300	20.3

TABLE XVIII.
Wawasee Blue Gills—April, 1929

Age	Number	Weight	Length
III	4	127	15.6
IV	2	149	16.6
VI	1	275	19.7

TABLE XIX.
Wawasee Blue Gills—6/18 and 7/5/29

Age	Number	Weight	Length
III	2	147	15.4
IV	1	300	19.7
V	1	305	20.0

Year groups I and II of the 1927 collection were taken by seine in the shallow water off the south end of Morrison's Island. The specimens of June 30, 1928, were taken by Mr. John Fleming of the Wawasee Hatcheries on a fly rod. All the 1929 individuals were taken in a 1½ inch mesh gill net. The different methods of collecting and the scarcity of material may account for the irregularities apparent.

ROCK BASS

The time of collection for rock bass ranged from July 15 to August 23 for 1926, from June 27 to July 25 for 1927, and from June 18 to July 1 for 1929. The five 1928 specimens were taken by seine June 19 and 20.

TABLE XX.
Wawasee Rock Bass—1926

Age	Number	Weight	Length
II	2	75	13.2
III	3	105	14.2
V	1	174	17.0
VI	1	365	22.7
VII	1	415	23.3

TABLE XXI.
Wawasee Rock Bass—1927

Age	Number	Weight	Length
I	14	55	5.6
II	5	38	10.5
III	5	98	14.5
IV	4	180	17.8
V	2	230	18.4
VII	2	290	23.4

TABLE XXII.
Wawasee Rock Bass—1928

Age	Number	Weight	Length
I	5	..	5.1
II	1	25	9.7
III	1	110	14.6
IV	4	218	18.6
V	1	275	20.3
VII	1	400	21.9

TABLE XXIII.
Wawasee Rock Bass—1929

Age	Number	Weight	Length
I	1	..	5.1
III	1	153	17.2
V	1	365	21.8

All members of the I group were taken by seine at the eastern end of the lake. The older classes of the 1926 and 1927 collection were furnished by fishermen. The single III and V specimens of 1929 were taken in a 1% inch mesh gill net.

The above data, meager as they are, make possible an interesting comparison with the results of Wright's (1929) study of the growth of the rock bass in northern Wisconsin. The longest specimen found by Dr. Wright had a length of 18.5 cm. His oldest individuals belonged to the XI year group. In the specimens collected from Wawasee, the maximum length was 23.7 cm., while the oldest year group represented was VII.

LARGE MOUTH BLACK BASS

The bass collected in 1929 were taken by a 1% inch mesh gill net. All specimens of the I and II group were taken by seine. The remainder of the specimens were furnished by fishermen.

In 1926, only two specimens were measured. One was in the V group, having a length of 34 cm. and a weight of 840 grams. The other had passed eight winters and had a length of 38.1 cm. Its weight was 1250 grams.

Fifteen specimens were taken in July, 1927.

TABLE XXIV.
Wawasee Large Mouth Bass—1927

Age	Number	Weight	Length
I	4	26	10.6
III	3	233	22.6
IV	2	375	27.7
V	6	594	30.9

In 1928, eight small specimens were taken by seine. On July 14, 5 individuals belonging to the I group, and having an average length of 8.4 cm. and average weight of 11 gm., were taken. At the same time, a single speci-

men of the II group was taken. It was 16.5 cm. long and weighed 90 grams. In the latter part of June, 2 belonging to the II group were taken. They had an average length of 14.8 cm. and an average weight of 69 grams.

In the latter part of April, 21 bass were collected. Five more were collected on June 18 and July 5.

TABLE XXV.
Wawasee Large Mouth Bass—1929

Date	Age	Number	Weight	Length
April	IV	19	402	26.2
April	V	2	675	29.2
6-18, 25	III	5	357	25.1
6-18, 25	IV	2	423	27.4

TABLE XXVI.
Wawasee Crappies

Date	Age	Number	Weight	Length
7-25-27	IV	1	215	20.6
7- 5-29	III	8	149	18.3
7- 5-29	IV	4	190	19.4

Of the fish taken in April, all but 1 or 2 of the smaller specimens in the IV group would have spawned.

BLACK CRAPPIE

The collections of crappies are given in Table XXVI.

SMALL MOUTH BLACK BASS

Three specimens were measured in July, 1926, and 7 in July, 1927.

TABLE XXVII.
Wawasee Small Mouth Bass

Date	Age	Number	Weight	Length
July, '24	V	1	400	27.3
July, '24	VI	1	820	33.7
July, '24	IX	1	1000	37.8
July, '27	IV	3	420	27.4
July, '27	VI	3	500	31.8
July, '27	VIII	1	1590	41.0

TABLE XXVIII.
Wawasee Pickerel

Date	Age	Number	Weight	Length
7-18-26	III	1	225	30.3
April, '29	IV	1	850	48.3
April, '29	V	2	2350	69.8
April, '29	VI	1	2725	83.7

PICKEREL

Five specimens were taken. See Table XXVIII.

LONGEARED SUNFISH

Three specimens were taken.

TABLE XXIX.
Wawasee Longeared Sunfish

Date	Age	Length
7-14-27	II	7.5
7-14-27	III	11.2
6-28-28	II	7.5

PAPAKEECHIE

Only a few scattered specimens were obtained from Papakeechie. This lake, which is artificial and privately owned, has rather stringent limitations on fishing. It is reputed to contain blue gills of a size smaller than the

average, although plentiful as to number. Bass fishing is good and the fish well grown. A collection of blue gills adequate for age study would, if available, be of interest. The belief is common that the blue gills are too plentiful because of insufficient fishing. A dense population of undersized blue gills would, of course, improve the situation among the bass.

TABLE XXX.
Papakeeche Blue Gills—8/8/1926

Age	Number	Weight	Length
V	2	94	14.7
VI	1	105	15.7

TABLE XXXI.
Papakeeche Perch—8/8/1926

Age	Number	Weight	Length
VI	1	223	23.0

TABLE XXXII.
Papakeeche Black Crappie—8/8/1926

Age	Number	Weight	Length
V	1	255	20.8
VI	1	227	20.3

TABLE XXXIII.
Papakeeche Large Mouth Bass

Date	Age	Number	Weight	Length
8-8-26	IV	1	210	22.3
7-14-26	VIII	1	1225	37.2
6-16-26	XVI?	1	2120	44.5
4-21-29	VIII	1	1050	37.5

INDIAN VILLAGE LAKES

Collections were made from the lower five lakes of the Indian Village chain. The channels by which the lakes communicate are large enough for passage by boat. Since the shores are in general marshy, none of the five lakes considered has been exploited for resort purposes. Consequently, the fishing is here less intensive than in most lakes. In the past, there has been a decreasing number of fish removed from the lakes by nets.

Collections from the Indian Village and Gordy Lakes were made in the early winter of 1928 at the spawning time of the ciscoe; from Indian Village and Duley Lakes on April 23, 1929; from Rider Lake June 22, 1929; from Gordy Lake July 23, 1929; and from Hyndman Lake August 12 and 13, 1929. The fish taken in 1928 were caught in a 1½ inch mesh gill net, and in a trammel net whose smaller mesh was 1½ mesh. All fish collected in 1929 were taken in a 1½ inch mesh net.

INDIAN VILLAGE

CISCO

Collections of ciscoes were made in the last four days of November, 1928, and July 23, 1929.

TABLE XXXIV.
Indian Village Cisco—November, 1928

Age	Number	Weight	Length
II	1	293	25.7
III	19	469	30.4
IV	15	530	31.9
V	8	613	32.7
VII	1	810	33.3

TABLE XXXV.
Indian Village—7/21/1929

Age	Number	Weight	Length
IV	9	553	32.4
V	7	615	33.4
VI	2	635	33.4

It should be noted that while the various groups have passed II, III, . . . winters, they have completed 3, 4, . . . growing seasons. The weight data for the 1928 collection are somewhat unreliable because of the admixture of both spawned and unspawned individuals.

BLUE GILLS

In 1929, 34 blue gills were collected April 23, and 14 on July 21.

TABLE XXXVI.
Indian Village Blue Gills—4/23/1929

Age	Number	Weight	Length
III	3	130	15.9
IV	28	150	16.6
V	3	186	18.4

TABLE XXXVII.
Indian Village Blue Gills—7/21/1929

Age	Number	Weight	Length
III	9	139	16.4
IV	3	182	18.0
V	1	200	18.1

CRAPPIES

Twelve crappies were collected on April 4, and 3 on July 21, 1929.

TABLE XXXVIII.
Indian Village Crappies—4/4/1929

Age	Number	Weight	Length
IV	8	168	18.5
V	3	220	20.6
VI	1	232	20.8

TABLE XXXIX.
Indian Village Crappies—7/21/1929

Age	Number	Weight	Length
III	3	150	18.3

LARGE MOUTH BLACK BASS

A single large mouth bass (4/23/29) of the IV group was 24.1 cm. long and weighed 320 grams.

DULEY

An April 23, 1929, a catch of 8 crappies and 53 blue gills was made. A 1½ inch mesh gill net was used.

TABLE XL.
Duley Blue Gills—4/23/29

Age	Number	Weight	Length
III	2	131	15.8
IV	42	138	16.3
V	5	155	16.9
VI	3	178	17.6
VII	1	220	19.1

Eight crappies of the III group had an average length of 18.0 cm., and an average weight of 140 grams.

RIDER

On July 20, 1929, a catch was made of 24 blue gills, 6 crappies, and 2 large mouth bass.

TABLE XLI.
Rider Blue Gills—7/20/29

Age	Number	Weight	Length
III	15	127	15.8
IV	7	158	16.9
V	2	205	18.7

The crappies belonged to the III group. Their average weight was 156 grams and their average length 18.8 cm. The two bass belonged to the V group. They had an average weight of 5.5 gm., and an average length of 27.4 cm.

GORDY

From November 26 to December 1, 1928, 13 cisco and 9 blue gills were taken. On July 23, 1929, a catch of 11 cisco and 25 blue gills was made. In the 1928 collection, a gill net and a trammel net with a 1½ inch smaller mesh were used. In 1929, the gill net alone was employed.

TABLE XLII.
Gordy Cisco—11/26 to 12/1/29

Age	Number	Weight	Length
II	1	265	26.4
III	12	452	29.6

TABLE XLIII.
Gordy Cisco 7/23/29

Age	Number	Weight	Length
IV	4	538	31.8
V	5	751	37.7
VI	2	940	39.4

TABLE XLIV.
Gordy Blue Gills—11/26/28

Age	Number	Weight	Length
III	4	127	15.6
IV	2	149	16.6
VI	1	275	19.7

TABLE XLV.
Gordy Blue Gills—7/23/29

Age	Number	Weight	Length
III	9	126	15.9
VI	14	166	17.5
V	2	199	18.7

HYNDMAN

Collections made August 12 and 13, 1929, included 46 blue gills and 11 ciscoes. A gill net was used.

TABLE XLVI.
Hyndman Blue Gills—8/12, 13/29

Age	Number	Weight	Length
III	33	136	16.5
IV	11	162	17.1
V	2	226	19.3

TABLE XLVII.
Hyndman Cisco—8/12, 13/29

Age	Number	Weight	Length
II	1	275	26.0
III	3	455	29.4
IV	5	434	29.0
VI	2	770	33.8

DEWART

Collections were made by means of gill nets, August 21 and 22, 1929. The collection included 45 blue gills, 7 crappies, 6 perch, and 1 large mouth black bass.

TABLE XLVIII.
Dewart Blue Gills—8/21, 22/29

Age	Number	Weight	Length
III	35	130	16.0
IV	9	160	17.7

One of the IV group specimens was not included in the computation of the averages. It had sustained an injury in which a considerable portion of the upper and lower jaw had been torn away on the left side. The wound was thoroughly healed, and the fish was in good condition. It was, however, somewhat undersized, having a weight of 112 gms. and a length of 15.9 cm. It was a female. The scales showed normal sculpturing.

Separate averages were computed for the 20 females and the 15 males of the III group.

TABLE XLIX.
Dewart, III Group—Blue Gills

Sex	Number	Weight	Length
♀	20	132	16.2
♂	15	128	15.8

The females show a slightly larger average for both weight and length.

CRAPPIES

The seven crappies all belonged to the III group. The average weight was 166 gms.; the average length 18.6 cm.

PERCH

The six perch, all members of the IV group, had an average weight of 355 gms. and an average length of 26.4 cm. All six were females. Dewart Lake is reputed for its perch, and these well grown specimens indicate the reputation to be well grounded.

LARGE MOUTH BASS

A single large mouth bass belonging to the IV group weighed 435 gms. and was 27.6 cm. long. The specimen was a female.

SPEAR

Attempts to secure data from Spear Lake proved singularly unfruitful. Below are the results from the three times the Lake was fished.

TABLE L.
Spear Lake—1929

	Age	Number	Weight	Length	Date
Large Mouth Bass.....	V	1	400	27.0	4-18-29
Large Mouth Bass.....	VII	1	660	31.4	4-18-29
Large Mouth Bass.....	IV	1	325	26.0	6-27-29
Blue Gill.....	III	1	150	17.0	7- 5-29
Crappie.....	III	2	167	19.4	7- 5-29

RIDINGER

An attempt at making a collection at Ridinger Lake June 20, 1929, netted only 3 blue gills and 3 crappies. All the specimens belonged to the III group.

TABLE LI.
Ridinger—6/20/29

	Weight	Length
Blue Gills.....	121	16.6
Crappies.....	166	19.0

BARBEE CHAIN

Of this chain of six lakes, Little Barbree, Big Barbree (Hammon), and Dan Kuhn (East) were fished for specimens. The results of the fishing in Dan Kuhn were negligible. A gill net was used in all collections.

The communicating channels are sufficiently large to be negotiated by row boats at all seasons.

BIG BARBEE (HAMMON)

The collections of July 15 and 29, 1929, consisted of 20 blue gills and 9 crappies.

TABLE LII.
Big Barbree Blue Gills—1929

Age	Number	Weight	Length
III	16	129	15.8
IV	4	175	17.8

TABLE LIII.
Big Barbree Crappies—1929

Age	Number	Weight	Length
III	6	145	18.4
IV	3	169	19.3

LITTLE BARBEE

Collections were made July 13 and 30, 1929. Fourteen blue gills and 6 crappies were taken. Gill nets were used.

TABLE LIV.
Little Barbree Blue Gills—1929

Age	Number	Weight	Length
III	13	119	15.6
IV	1	170	17.6

TABLE LV.
Little Barbree Crappies—1929

Age	Number	Weight	Length
III	2	131	17.7
IV	3	144	18.6
V	1	197	20.0

DAN KUHN (EAST) LAKE

An attempt to make a collection on July 31, 1929, resulted in the capture of only four blue gills.

TABLE LVI.
Dan Kuhn Blue Gills—1929

Age	Number	Weight	Length
III	2	128	16.6
IV	2	145	17.6

LITTLE CHAPMAN (LITTLE EAGLE)¹

Twenty-five blue gills were taken from Little Chapman Lake July 6, 1929. A gill net was used.

TABLE LVII.
Little Chapman Blue Gills—7/6/29

Age	Number	Weight	Length
III	12	124	15.9
IV	13	152	16.9

The presence of such a large percentage of the IV group suggests the possibility that many of the III group were small enough to escape the net.

CENTER

Eighteen blue gills and one crappie were taken from the Center Lake July 2, 1929. The collection was made by means of a gill net.

TABLE LVIII.
Center Blue Gills—7/2/27

Age	Number	Weight	Length
III	15	126	15.6
IV	3	148	16.5

The crappie was from the III group. Its weight was 173 gms., and its length 18.7 cm.

PIKE

Although this lake was visited on several occasions, the total collection was quite small. Pike Lake seems to be infested with a considerable number of dogfish, gar-pike, carp, and suckers. The collections of July 8, July 10,

¹ The name Little Eagle properly includes two lakes, Big Chapman and Little Chapman. Draining projects have lowered the level of Little Eagle, dividing it into two smaller and definitely separated bodies.

and August 6, 1929, contained 5 blue gills, 5 crappies, 2 pickerel, and 1 silver bass.

TABLE LIX.
Pike—1929

Name	Age	Number	Weight	Length
Blue Gill	III	5	125	15.9
Crappie	III	5	160	19.8
Pike	IV	2	1190	53.5
Silver Bass	III	1	365	25.1

LITTLE PIKE

Little Pike is a small lake communicating with Pike Lake by a channel, easily navigable in a row boat. The shore line is mostly marshy, and the vegetation abundant in the littoral region. As is the case with Pike Lake, Little Pike seems to have a considerable population of carp and suckers. The lake is highly reputed for pickerel fishing.

Collections were made July 10 and August 6, 1929. The two collections contained 12 crappies, 9 blue gills, 4 pickerel, 3 silver bass, and 1 large mouth bass. Since the number of specimens is so small, the two samples have been combined in the presentation of data.

TABLE LX.
Little Pike Crappies—1929

Age	Number	Weight	Length
IV	6	165	19.6
V	4	215	22.3
VI	2	320	24.2

The crappies from Little Pike are of a larger size than those found in the collections from most lakes.

TABLE LXI.
Little Pike Blue Gills—1929

Age	Number	Weight	Length
III	6	119	15.2
IV	3	131	16.1

TABLE LXII.
Little Pike Pickerel—1929

Age	Number	Weight	Length
IV	1	825	45.7
V	2	795	45.0
VI	1	1375	45.6

Three silver bass of the III group had an average weight of 560 gm. and an average length of 28.6 cm.

A large mouth bass weighing 425 gm. and 26.4 cm. long belonged to the IV group.

WINONA (EAGLE)

Samples from Winona before 1929 were small and scattered. In 1929, a total of 129 blue gills and 54 crappies were collected. Most of the specimens of the year group III and above were taken by means of a gill net. The smaller ones were taken by hook and line.

BLUE GILLS

Only four blue gills were obtained before 1929. Table LXIII.

TABLE LXIII.
Winona Blue Gills—1925-26

Date	Age	Number	Weight	Length
8-19-25	II	1	28.2	11.0
7-31-26	I	1	12.5	8.0
7-24-26	II	2	...	11.9

TABLE LXIV.
Winona Blue Gills, I Group—1929

Date	Number	Weight	Length
7-14	7	12	8.1
8-1	2	18.5	9.1

Nine I group specimens were taken in 1929. Table LXIV.

The size of these specimens is perhaps too great, since they were taken by hook and line.

A total of 80 specimens in the II group were taken in four collections.

TABLE LXV.
Winona Blue Gills, II Group—1929

Date	Number	Weight	Length
6-29-29 ¹	21	...	11.5
7-13-29	15	43	11.7
8- 1-29	41	42	11.6
8- 8-29	3	42	11.8

The data do not indicate a very rapid growth in July and early August. Such growth may be obscured by selective sampling.

The 23 blue gills of the III group have been divided into two groups, one collected during the month of July and the other during the first nine days of August.

TABLE LXVI.
Winona Blue Gills, III Group—1929

Month	Number	Weight	Length
July	10	115	15.0
August	13	108	15.1

TABLE LXVII.
Winona Blue Gills, IV-V Groups—1929

Age	Number	Weight	Length
IV	16	138	16.9
V	1	183	19.1

CRAPPIES

A single crappie was taken August 19, 1925. It belonged to the II group and had a weight of 82 gms. and a length of 15.6 cm.

Only one II group specimen was taken in 1929 (July 19). It weighed 75 gms. and was 14.9 cm. long.

Eleven III group crappies were taken in July and 14 during the first nine days of August.

TABLE LXVIII.
Winona Crappies, III Group—1929

Month	Number	Weight	Length
July	11	141	18.2
August	14	151	18.4

¹ These scales and measurements for specimens were furnished by Miss Ulrey. Weights were given to the nearest half ounce.

In the IV group, 16 were collected in July 15 in early August.

TABLE LXIX.
Winona Crappies, IV Group—1929

Month	Number	Weight	Length
July	10	228	21.1
August	15	246	21.2

TABLE LXX.
Winona Crappies, V Group—1929

Month	Number	Weight	Length
August	3	303	22.8

PERCH

Thirty-three perch were collected by means of a seine August 14 and 19, 1925.

TABLE LXXI.
Winona Perch—August, 1925

Age	Number	Weight	Length
0	15	1.9	5.2
I	10	9.8	8.6
II	8	27.3	12.2

The average weights are given to the nearest tenth of a gram. These specimens were weighed on beam arm balances at the Biological Station. Although it is possible that some of the smaller perch of the O group escaped through the meshes of the seine, it is still evident that the perch enjoys a good growth in its first season. The weight of the O fish is less than might be expected in fish of their length.

LONGEARED SUNFISH

Two collections of longeared sunfish were made. In 1927, 17 specimens were taken on June 22 and 27. In 1929, 8 were taken on July 14. The 1927 fish were taken by a seine; the 1929 fish by hook and line.

TABLE LXXII.
Winona Long Eared Sunfish—1927

Age	Number	Weight	Length
II	9	16	7.3
III	4	28	8.1
IV	2	33	9.2
V	2	34	9.4

TABLE LXXIII.
Winona Long Eared Sunfish—1929

Age	Number	Weight	Length
II	5	13	7.7
III	3	41	11.2

LARGE MOUTH BASS

Dr. Scott furnished data from 5 large mouth black bass caught by him.

TABLE LXXIV.
Winona Large Mouth Bass

Date	Age	Weight	Length
7- 4-26	IV	486	32.4
7- 4-27	VII	1746	40.6
7-20-27	V	650	33.0
8-17-27	VIII	1250	40.6
7- 4-27	V	1025	40.3

ROCK BASS

Only one rock bass was obtained from Winona. This specimen, taken July 31, 1926, weighed 187 gm. and was 17.1 cm. long. It belonged to the year group V.

SILVER LAKE

Silver Lake was fished with a net August 10 and 17, 1929. Fifteen blue gills and 2 crappies were collected.

TABLE LXXV.
Silver Blue Gills—1927

Age	Number	Weight	Length
III	14	135	16.5
IV	1	163	18.3

The 2 crappies belonged to the III group. They had an average weight of 136 gm. and an average length of 17.6 cm.

RELATIONSHIP BETWEEN WEIGHT AND LENGTH

It has been found that within reasonable limits of variation, the weight of a fish varies directly as the cube of its length; i. e.:

$$\frac{W}{L^3} = c, \quad \text{or}$$

$$W = cL^3 \quad \text{where } c \text{ is a constant.}$$

Where W is expressed in grams and L in centimeters, it is found convenient to introduce another constant K where

$$\frac{K}{100} = c.$$

The equation then becomes

$$W = \frac{KL^3}{100}.$$

The value of the constant K is in general characteristic for a given species. Its variations may then be taken as indicative of variations in condition of the different individual fishes. Because of its significance in indicating the condition of fishes, K has come to be termed the "coefficient of condition."

The chief factors producing variations in the value of "K" are sexual state and feeding conditions. Where there is no distortion of the relation-

ship from sexual development, K may be taken to indicate the "fatness" or degree of well being of the individual. Clark¹ (1928) found the weight length factor to reflect the fat content of the California sardine. The factor values were found to decrease from December to May for larger fish, and from December to January for the smaller. Todd (1915) found that condition in the plaice varied according to food conditions, and that the amount of molluscs available seemed to be the factor of greatest importance.

Hecht (1916) found that the weight-length relationship did not vary with increase in size, and concluded that form was constant throughout life. Tjurin (1927) found that when the relationship between length and weight has been determined and plotted on a logarithmic scale, the weight of *Coregonus tuqun* (Pallas) can be calculated accurately from the body length. Van Oosten (1926) found the calculated values of the weight of lake herrings to vary only slightly from the actual values. The greatest variations of the true value from the calculated value was found in the largest size group. Menzies (1927), however, found the value of K to increase with age in the spring and summer fish groups of the Scottish salmon. He further found the longer fish within a year class to be the fatter. Clark's data on the sardine indicate the reverse: that smaller specimens within the year class are the fatter.

Average values of K for certain of the collections considered in this study appear in Tables XCII to XCVI. In comparing values for collections from different lakes and for different collections in the same lake, it is well to keep in mind the fact of seasonal variation in condition. The data here at hand afford no basis for determining the nature of such variation. For this purpose, it would be necessary to have a series of collections ranging in time throughout the entire year. The data do indicate slightly a tendency for K to increase in value as the summer proceeds.

BLUE GILLS

No definite trend of variation of K from one year class to the other is evident from the data. In 21 samples, the III class occurred along with specimens from other year groups. In 13 of the 21 cases, the III had an average value for K greater than any other year group; i. e., in 62% of the cases. Similarly, in 5 out of 20, or in 25% of the cases, the IV group held the maximum average value of K and in 2 out of 9, or 22%, the V group possessed the greatest average value. The II group appears with other year classes 5 times, but in no instance has the greatest value of K for the collection. The VI group appeared twice, but showed a maximum value for K in only one sample where the year class had only one representative. Only one specimen in the VII group was encountered. The lowest individual values for K were found in the II group.

An interesting case of an unusually high coefficient of condition was encountered in Tippecanoe Lake. A blue gill of the III group taken August 20, 1929, weighed 186 gm., although its length was only 15.9 cm. The value for K was 5.348. For the total group, the average weight was 139, and the average length 15.9 cm. The caudal peduncle was much shortened. The vertebrae of the caudal portion were reduced in size. There was no indica-

¹This publication contains a bibliography of papers dealing with the problem of the relation of weight to length in fishes.

tion of any abnormality resulting from injury. This was the only instance of such a great variation from the average condition.

The disturbing factor of seasonal variation as affecting comparisons made at different dates from different localities has been mentioned. Although based on few specimens, the samples from Indian Village and Gordy Lakes indicate respectively a falling from April and from midwinter to July. The samples taken from Winona in 1929 indicate no consistent change in the values of K from July to early August.

Certain comparisons are, however, possible. It is obvious that the blue gills from Wawasee are uniformly in excellent condition. The August, 1929, collections from Hyndman, Tippecanoe, Dewart, Winona, and Silver Lakes were taken within a space of time small enough that they may be considered comparable. The first two show a value of K definitely higher than the last three. In the case of the five lakes of the Indian Village chain, the collections were scattered too much through the different seasons to serve satisfactorily as a basis for comparison. On the whole, the fish from Hyndman Lake seem to have the highest values for K, but it must be noted that no collections taken from any of the other lakes of that group at the same time are available for comparison.

CRAPPIES

The material on the whole is too scanty for purposes of comparison. It is of interest to note that the crappies from Little Pike Lake, which show unusually low value for K, were nevertheless the largest specimens both in weight and length encountered in any collections.

CISCOES

Since the 1928 collections were made at the spawning time, the values of K were not computed. These collections contained both spent and unspawned specimens. The specimens from the Hyndman Lake collection showed the beginning of the pre-spawning development of the gonads. This circumstance probably accounts for the higher values from this lake.

A comparison of Van Oosten's (1928) values for this species reveals striking differences.

TABLE LXXVI.

Age ¹	Lake Huron	Indian Village Lakes ²
I and II	1.11	
II	1.11	1.56
III	1.13	1.79
IV	1.16	1.66
V	1.19	1.69
VI		1.64
VII		1.54

¹ The ages as given by Van Oosten are modified so as to be comparable with those of the Indian Village fish.

² In order to render the data from the two sources comparable, I have rounded off Van Oosten's values to three significant figures, moved the decimal places two places to the right, combined the values for the two sexes, and in the cases where he presented data for more than one group of the same age, I have combined these to arrive at an average. Due to the great degree of uniformity of his data, these operations produced little alteration in the values. In his summary Van Oosten gives as the value of K for *L. artedi* the constant 0.01126 or 1.13 by the method of notation employed in this paper. The above modified figures for the Lake Huron ciscoes are based on data presented in Table 44, page 377 of Van Oosten's (1928) paper.

The values of K for the Indian Village fish are from 41% to 58% greater than those for the corresponding year groups from Lake Huron. Whatever the factors producing such great differences, they must be potent. First there exists, of course, the possibility of a racial difference. There is reason to believe that the Indian Village ciscoes have long existed as an isolated group. Their environment is quite unlike that of the Lake Huron group. Scott (1931) points out that the Indian Village ciscoes live under conditions of temperature and oxygen tension which have in the past been considered impossible for any members of the species. The lakes are shallow, the summer water temperature high at all depths, and oxygen is absent from the lower strata during the summer months. Circumstances which force a species to adapt itself to a new set of environmental conditions are doubtless conducive to the formation of racial differences. It should be remembered further that the Indian Village Lakes lie at a much lower latitude than does Lake Huron. There results a higher average water temperature for the more southernly lakes, and a longer growing season for their fish population. Again, feeding conditions are more favorable in the Indiana lakes as quantitative studies have brought out.

Koelz was unable to make a precise taxonomic determination on specimens sent him from Indian Village and Gordy Lakes because of the small number of individuals in the sample. He suggested that the ciscoes of these lakes are probably the same as those reported by Jordan from Lake Tippecanoe as *Leucichthys artedi cisco*. A racial study of the ciscoes of Indiana lakes should prove of value.

PERCH

A small collection from Winona Lake taken August 14 and 19, 1925, affords an opportunity for comparison of the first three year classes. These specimens were weighed accurately, and their lengths carefully measured by use of dividers. A marked increase in the value of K from the O to the I group is indicated. The change from the II to the III group is less pronounced.

The 1926 perch from Wawasee show a fair degree of uniformity from the II to the V group.

The small values for K in both the I and II groups of the 1929 collections is striking. The collections were made at the same part of the lake in 1927, 1928, and 1929. Hence, the 1929 II group might be considered a continuation of the 1928 I group. Nevertheless the values of K for this year group were 1.50 and 1.30 for 1928 and 1929, respectively. The opinion that environmental factors are responsible is given support through the circumstance of low values for both year classes represented in the 1929 samples.

The six perch taken from Dewart Lake August 21 and 22, 1929, were not only the largest as to weight and length taken in any collection, but also show an unusually high weight for their length.

Other Species.—The values of K for the large mouth bass, the small mouth bass, and the pickerel, respectively, in Wawasee are 2.18, 2.04, and .68. The average value of K for the various silver bass collected is 2.12.

VARIATION IN LENGTH

On the whole, the variations in length from lake to lake are not great. In making comparisons, it is well to keep in mind the number of specimens, the date of collection, and the method of capture. Tables LXXXII to XCI summarize by species the different collections.

BLUE GILLS

In length, as in weight, the Wawasee fish show better growth than those of other lakes. The advantage is first apparent in the IV group and seems to depend chiefly upon the better growth of Wawasee blue gills during and beyond the fourth summer.

It is to be noted that there is no demonstrable correlation between the average length of a sample and the average value of K. The lakes having the better grown fish with respect to length do not necessarily have the fish showing the best "condition." It is, of course, possible that the lack of correlation is only an apparent one. The collections were made over a considerable period of time, and it is further easily conceivable that the differences resulting from the method of collection might be sufficiently large to obscure variations which might be brought to light were all collections made within a short period of time and by the same gear.

There are certain food conditions in Wawasee which may in part explain continued good growth in the blue gills. It has been shown (Scott *et al.*, 1928) that, during the summer months, there is an unusually plentiful population of large Chironomid larvae, and that this population is particularly dense in a belt lying approximately between the 10 and 15 meter contour lines. That the food material is not unavailable due to chemical conditions has been demonstrated through gas analyses which show sufficient dissolved oxygen to support life easily in all except the lower strata of the region.

During July, the blue gills congregate in this region of deeper, cooler water and plentiful food supply. Those seeking to catch blue gills of a good size fish "in about forty feet of water" and with their baited hooks between one and three feet above the bottom. During the latter part of July and in August, large blue gills are seldom taken elsewhere (occasionally they can be taken on a fly). I have never known individuals smaller than those of the III group to be caught in this deep water. The stomachs of the blue gills taken in the 10-15 meter belt contain many large chironomid larvae.

Such an abundance of bottom food as occurs in Wawasee is not found regularly in other lakes. Comparison with a similar study of Tippecanoe shows that the bottom of the latter lake has a scantier supply of food forms. In this instance, the much greater supply of plankton makes up in part the deficiency. Mr. Floyd Carpenter, who has collected chironomid larvae extensively, has told me that in most lakes these forms are quite sparse as compared to Lake Wawasee.

A study of the stomach contents of blue gills¹ has showed that in July and August small crustaceans (chiefly Cladocera) constitute the chief element of their diet. Large chironomid larvae, if available in quantity, should, in the matter of size at least, be superior to small crustaceans as food for larger fish. It would be expected that the fish would avail themselves of the food

¹ From unpublished data furnished by Dr. Will Scott.

more easily taken in large quantities, and that they might congregate in the region of such an abundant food supply.

The excellent food conditions in Wawasee are brought forth graphically in the following table which gives the total amount of bottom food organisms in different waters. The material for the table with the exception of that concerning Lake Wawasee appears in Adamstone's (1924) report on the bottom fauna of Lake Nipigon. The values for the different zones in Wawasee were calculated from data from the report by Scott *et al* (1928) on the bottom fauna of that lake.

TABLE LXXVII.
Quantity of Food Organisms in Bottom Fauna in Different Waters

Lake	Zone (Meters)	Pounds per Acre (Dry Wt.)
Illinois River.....		261
Connecting lakes of Illinois River.....		155
Lakes N.E. Illinois.....		82.8
Oneida.....		245
Mendota.....	0—1	60
Mendota.....	1—3	64
Mendota.....	8—20	42.9
Green Lake.....	0—1	7.75
Green Lake.....	1—10	14.2
Green Lake.....	10—20	26.6
Green Lake.....	20—40	29.9
Green Lake.....	40—66	27.6
Nipigon.....		5.23
Wawasee ¹	0—2	218.5
Wawasee ¹	2—4	213.3
Wawasee ¹	4—23	103.0

The Illinois River with its connecting lakes, and Lake Oneida excel Wawasee in the quantity of food forms. On the other hand, Wawasee has a much richer fauna than the lakes of northeastern Illinois, Lake Mendota, Green Lake, and Lake Nipigon. The poorer fauna of the northern lakes is suggestive of the possible effect of latitude. The degree of effectiveness of that factor is, however, rendered problematic through the undoubted importance of such factors as fertility and general geological make-up of the surrounding land, the type of bottom, the plant population, and the actual form (area, slope, depth) of the different lakes.

CRAPPIES

Variation from lake to lake is not marked. As further impediments to making comparisons stand the small size of the collections and the scant representation of the year class above the III group. The largest crappies encountered were taken from little Pike Lake. Well grown crappies were also found in Winona Lake.

PERCH

Most of the perch studied were taken from Wawasee. The collections agreed well from year to year. There was also close agreement between Wawasee samples and collections of the early year classes from Syracuse,

¹The high values for Wawasee are in part due to the presence of large numbers of molluscs particularly *Goniobasis* and *Sphaerium* which give a large dry weight.

Tippecanoe, and Winona Lakes. The largest perch studied were taken from Dewart Lake.

In many lakes, perch are found in abundance, but large ones are rare. Large perch are seldom taken in Winona or Tippecanoe. In Wawasee the individuals of greater size are fairly common, and Dewart Lake is highly reputed for its perch. It is probable that the variation in the perch fishery from lake to lake results not so much from variations in growth rate as it does upon factors which tend to eliminate most of the individuals before they had attained an advanced age. There remain, of course, the possibilities of a change in growth rate or of habits in the adult which bring about immunity from capture by ordinary fishing methods. In the first instance, it would be difficult to account for the absence of the stunted specimens from the samples.

At this point a comparison with Harkness' (1922) results in his growth study of the yellow perch of Lake Erie is of interest. The following table gives the lengths of the different year classes in Lake Wawasee and Lake Erie.

TABLE LXXVIII.

Age	0	I	II	III	IV	V	VI	VII
Wawasee.....	3.9	8.6	12.9	16.7	19.8	22.0	23.0	
Erie.....	4.4		14.4	16.8	18.7	21.7	23.4	24.4

Harkness states that his material was obtained in the summer and autumn. The perch from Wawasee were, except for a very few specimens, taken in midsummer months, and may as a whole be considered typical for July. It is likely, then, that the Lake Erie fish were taken somewhat later in the growing season. This circumstance would give them a slight advantage over the Wawasee perch, an advantage which would tend to show itself in the first few year classes but would be negligible in the older groups.

It may be seen that the trend of growth of perch in the two lakes is quite similar. The few specimens taken from Dewart Lake were better grown than any from either Erie or Wawasee.

Cisco.—The largest ciscoes were found in Gordy Lake. No consistent variation from lake to lake is apparent.

A comparison with the data presented by Clemens (1922) and Van Oosten (1928) for the same species indicates a much more rapid growth and a greater size for the Indiana fish.

The following table gives the comparison between the length values for the fish from Saginaw Bay, Lake Huron, from Lake Erie, and from the Indian Village Lakes (Indian Village, Gordy, and Hyndman).

TABLE LXXIX.

Year Class.....	I	II	III	IV	V	VI	VII
Saginaw Bay ¹	18.5	21.8	23.5	24.4	25.8	27.4	29.2
Erie.....	12.5	16.0	19.9	21.5	23.5	25.5	27.5
Indian Village.....		26.0	30.1	31.6	34.2	33.6	37.4

¹ These length averages are taken from Table 43, page 374 of Van Oosten's (1928) paper. The ages have been altered to make them comparable to the Indian Village fish. In the comparison the Lake Huron fish are given a slight advantage since the Indian Village samples contained some specimens which were taken in the summer, and had not completed the season's growth.

When it is remembered further that the Indian Village fish are much heavier proportionate to length than those from Lake Huron, the difference in actual size between those two groups is more striking.

The ciscoes from Lake Erie show a growth far below that of either the Bay City or the Indian Village specimens.

The matter of the possible causes of the differences has already been discussed.

OTHER SPECIES

Large Mouth Black Bass.—The collections were small and scattered. The samples from Wawasee are fairly consistent within themselves. A single XVI(?) group specimen from Papakeeche was the oldest one studied.

Small Mouth Black Bass.—The few specimens give no basis for comparison.

Longeared Sunfish.—The specimens in all collections were small and showed slow growth.

Rock Bass.—All but three of the specimens were taken from Wawasee and have been discussed previously.

White Bass.—No comparison can be based on the data at hand.

Pickarel.—A rather rapid growth is indicated in the few specimens from Wawasee.

TABLE LXXX.

SPECIES	YEAR CLASS										
	0	I	II	III	IV	V	VI	VII	VIII	IX	XVI?
Perch.....	66 (9)	390 (51)	240 (32)	36 (5)	21 (3)	3 (.43)	1 (.13)				
Blue Gills.....		26 (4)	192 (26)	281 (39)	182 (25)	37 (5)	7 (.96)	1 (.14)			
Crappies.....			2 (1)	72 (47)	63 (41)	12 (8)	4 (3)				
Long-eared Sunfish....		1 (3)	18 (53)	9 (26)	3 (9)	3 (9)					
Large Mouth Black Bass.....	9 (10)	22 (24)	4 (4)	8 (9)	29 (32)	13 (14)		2 (2)	4 (4)		1 (1)
Small Mouth Black Bass.....					3 (30)	1 (10)	4 (40)		1 (10)	1 (10)	
Rock Bass.....		26 (37)	17 (24)	9 (13)	8 (11)	7 (10)	1 (1)	3 (4)			
Silver Bass.....			3 (33)	6 (67)							
Cisco.....			3 (3)	34 (35)	33 (34)	20 (21)	4 (4)	3 (3)			
Pickarel.....				1 (7)	6 (40)	6 (40)	2 (13)				

REPRESENTATION OF THE DIFFERENT AGE GROUPS

Table LXXX presents the proportions of the various year groups in the total collections of the different species by both actual numbers and percentages. To a large extent the figures are of no value for comparison, being largely the results of the different methods of sampling. The data are presented merely to show the actual age composition of the collections and to indicate the relative scarcity of older specimens. Groups taken by the same fishing methods may, however, be compared.

Perch.—The I and II groups were taken for the most part by the same method, but are not comparable with older year classes. There is a 37% decrease in numbers from the second to the third summers. Among the older groups it will be noticed that fish more than four years old are rare.

Blue Gills.—The smaller individuals of the III group could doubtless pass through the net. The proportion of this year class with respect to the older groups should, then, be larger. There is a marked falling off from the IV to the V group, and specimens above the latter age are quite rare.

Crappies.—Here as with the blue gills it is likely that the smaller III group specimens escaped the net. Fish above four years of age are not numerous.

Longeared Sunfish.—The few specimens at hand were not taken by any one method.

Large Mouth Black Bass.—They are well represented in the IV and V groups. Some, it seems, survive to a quite respectable age. The net used could not take the large specimens. The lower limit of selection is uncertain, but it is probable that the III group was affected most.

Small Mouth Black Bass.—All were taken on a casting rod. The data are almost negligible, but it is probable that the age distribution is similar to that of the large mouth bass.

Rock Bass.—Specimens beyond the V group were scarce. On the whole, the situation resembles that of the blue gills and crappies.

Silver Bass.—No adequate data are available. For this species the individuals studied are quite small.

Cisco.—All groups, except for selection by the net, are well represented as far as the six year old fish. The greatest drop in numbers comes from the V to the VI group.

Pickrel.—It is certain that individuals of this species reach an age well beyond that of any of the specimens studied here. While the largest pickerel taken in any of my collections weighed only about eight pounds, some individuals are known to grow to a weight greater than twenty-five pounds. By virtue of their size, these large fish are seldom taken.

AGE AND LEGAL LENGTH LIMITS

The legal length limits for the different species studied in this paper, as fixed by the fish and game laws of the state of Indiana are:

Blue Gill	5 in.
Rock Bass	5 in.
Black Crappie	6 in.
Longeared Sunfish	5 in.
Large Mouth Bass	11 in.
Small Mouth Bass	11 in.
Silver Bass	10 in.
Ringed Perch	7 in.
Pickereel	15 in.
Cisco	none

The limits are for total length, not for standard length.

Blue Gills.—The legal length is attained in the third growing season (II group). No specimens were taken earlier in the season than in late June. At this time, almost all are of legal size. No. I group specimens encountered were of legal length; nor were any III group individuals below five inches.

Rock Bass.—Here the conditions are similar to those of the blue gill. The individuals of the II group are somewhat slower in reaching the required length than in the blue gills, but all are above five inches in the III group samples.

Black Crappies.—The two youngest specimens examined were members of the II group taken from Winona Lake. Both were above six inches. They must have attained legal length early in the third summer.

Longeared Sunfish.—It is doubtful whether legal size is reached before the fourth growing season, and some individuals in the III, IV, and V groups will scarcely pass the scrutiny of the law.

Ringed Perch. The legal size of seven inches is not reached before the third summer (II group). The collections of this year group are composed of a mixture of individuals below and above legal length. The percentage above seven inches increases as the season advances. In the III group collections, practically all specimens are above legal length.

Large Mouth Black Bass.—A collection from Wawasee taken in April, 1929, showed that at the beginning of the fifth summer almost all of the individuals were above eleven inches. It is probable that in Wawasee most large mouth bass reach legal size during the fourth summer (III group). There is little data from other lakes, but they probably do not vary much from the conditions found in Wawasee.

Small Mouth Black Bass.—The youngest individuals examined were taken at about the middle of the fifth growing season (IV group). They were above legal size.

Juday and Schneberger (1930) report that in the Wisconsin lakes where the length limit is ten inches, "the large and small mouth bass rarely reach a length of ten inches before the fifth year and only 25% to 50% of them attain that size in the fifth year. Even some of the six year old specimens

had not reached that length." Their report indicates a better growth for the black bass in Indiana lakes.

Silver Bass.—It is difficult to make a determination from the few specimens at hand. It appears that the silver bass is of legal size in its fourth summer (III group), and that that size may possibly be attained in the third summer.

Pickereel.—The single specimen of the III group was under legal size while those of the IV group were above that size. It would appear that legal length is attained late in the fourth growing season or early in the fifth.

Cisco.—Since this fish is rarely taken except in nets, the law prohibiting netting makes a size protection unnecessary.

SUMMARY

1. This growth study is based upon 1,955 specimens, including 10 species and collected from 20 lakes in three drainage areas.

2. The determination of the ages was based upon a study of the scales. The validity of the method is assumed on the basis of investigations which have been made by previous workers.

3. The data presented include age, length, weight, and, in some instances, the value of K (coefficient of condition).

4. Tables are presented showing comparative lengths of the various species in the different collections. On the whole, the variation from lake to lake is not great. In many instances, the agreement between different lakes is very close. The blue gills from Lake Wawasee enjoy a growth above the average. The better size attained by the Wawasee fish seems to result from continued good growth in the fourth and succeeding summers. The method of obtaining the sample exerts considerable influence on the nature of the sample.

5. Increments of growth for periods within the growing season were determined in the I and II groups of the perch in Lake Wawasee for the summers of 1927, 1928, and 1929.

6. The value of K depends partly on the date of collection. Certain lakes nevertheless show a definitely higher value for K for blue gills than do others.

7. No definite trend is apparent in comparing values for K in the different year groups. In the blue gills, where no data below the II group were available, the maximum value for K occurred most frequently in the III group. A small collection of perch from Winona Lake indicated a distinct rise in the value of K from the O to the I group.

8. The collections of I and II group perch from Wawasee show considerable variation in the value of K from year to year. The average values for these year groups in the 1929 samples are greatly below those of the three preceding years. The length averages for these fish are the equal of those of previous seasons.

9. Food conditions affecting the older fish are suggested as a possible factor in the continued good growth of the older blue gills from Lake Wawasee.

10. The greater number of the larger blue gills and crappies belonged to the III group. Members of the IV group were usually found, while those of higher groups were rare. The maximum age group encountered for each of

the ten species was: blue gill, VII; crappie, VI; longear sunfish, V; rock bass, VII; large mouth black bass, XVI(?); small mouth black bass, IX; silver bass, III; cisco, VII; pike, VI; yellow perch, VII.

11. Comparisons with growth data presented by Wright (1929) on the rock bass and by Clemens (1922) and Van Oosten (1928) on the cisco (lake herring) indicate that the Indiana fish grow more rapidly and attain a greater size. In the case of the lake herring, the values of K were in each age group more than 40% higher for the Indiana than for the Huron fish. Juday and Schneberger's (1930) report on the game fishes of Wisconsin lakes indicates that the large and small mouth black bass grow more rapidly in Indiana lakes. A suggested explanation is that the difference in latitude produces a corresponding difference in factors influencing growth—average water temperature, food conditions, and length of the growing season—with the Indiana fish living under the more favorable conditions.

Relatively close agreement in the nature of growth is found between the yellow perch of Lake Erie (Harkness, 1922) and Lake Wawasee.

BIBLIOGRAPHY

ADAMSTONE, F. B.

1924. The distribution and economic importance of the bottom fauna of Lake Nipigon with an appendix on the bottom fauna of Lake Ontario. Univ. of Toronto Stud., Biol. Ser., No. 25, pp. 33-100.

BAUDELLOT, E.

1873. Recherches sur la structure et le développement des écailles des poissons osseux. Arch. de Zool. Exp. et Gen. Vol. II pp. 87-244 and pp. 427-480. Pls. V-XI.

BLEGVAD, H.

1927. On the annual fluctuations in the age composition of the stock of plaice. Rep. Dan. Biol. Sta. Vol. XXXIII, 1927, 18 pp.

BOLEN, HOMER R.

1925. The relation of size to age in some common freshwater fishes. Proc. Ind. Acad. Sci., Vol. XXXIII, 1923 (1924), pp. 307-309.

BORLEY, J. O.

1912. Report on the experimental transplantation of plaice to the Dogger Bank. Mar. Biol. As. Intern. Invest. Report IV (Cd 6125).

CLEMENS, WILBERT A.

1922. A study of the ciscoes of Lake Erie. No. 20, Pub. of Ont. Fisheries Res. Lab., I-IX, No. 2, pp. 25-37.

CREASER, CHARLES W.

1926. The structure and growth of the scales of fishes in relation to the interpretation of their life history, with special reference to the sunfish, *Eupomotis gibbosus*. Univ. Mich. Mus. of Zool. Misc. Pub. No. 17.

CROZIER, W. J., AND HECHT, SELIG.

1914. Correlations of weight, length and other body measurements in the weak fish, *Cynoscion regalis*. Bul. U. S. Bur. Fish. Vol. XXXII, 1913 (1915), pp. 139-147, 4 figs.

DAHL, KNUT.

1909. The assessment of age and growth in fish. Inter. Rev. Hydro. Vol. II, 1909.

- FOX, E. L.
1922. Moorland waters and trout food. *Salmon and Trout Mag.*, No. 29, pp. 159-162, 1922.
- GRAHAM, MICHAEL.
1929. Studies of age-determination in fish. Part II. A survey of the literature. *Min. of Agr. and Fish., Fish. Invest. Ser. II, Vol. XI, No. 3*, 1928 (1929).
- HARDY, A. C.
1924. The herring in relation to its animate environment. *Min. of Agr. and Fish., Fish. Invest., Ser. II, Vol. VII, No. 3*, London, 1924.
- HARKNESS, W. J. K.
1922. The rate of growth of the yellow perch in Lake Erie. No. 29, *Pub. of Ont. Fisheries Res. Lab., I-IX, No. 6*, pp. 87-97.
- HECHT, SELIG.
1916. Form and growth in fishes. *Contr. from Zool. Lab. of Mus. Comp. Zool., Harvard College*, No. 275.
- HERTLING, H.
1928. Untersuchungen über die Ernährung von Meeresfischen. I. Quantitative Untersuchungen an Pleuronektiden und einigen anderen Fischen der Ostsee. *Ber. D. W. K. für Meeresforsch., N. F., Bd. IV, Heft 2*.
- HOFFBAUER, C. H.
1898. Die Altersbestimmung des Karpfens an seiner Schuppen. *Allgemeine Fischerei Zeitung*, No. 19.
- HUITFELDT-KAAS, H.
1927. Studier over Aldersforholder og Veksttyper hos Norske Ferskvannsfisker. *Nationaltrykkeriet, Oslo*, 1927.
- HUTTON, J. ARTHUR.
1921. The literature of fish scales. *Salmon and Trout Mag.*, No. 26, 1921, pp. 203-217.
- JENSEN, AAGE J. C.
1928. The relation between the size of the plaice stock and the quantity of "First Class Plaice Food" in certain parts of the Limfjord. *Rept. Dan. Biol. Sta.*, 1928, pp. 87-98.
- JOHANSEN, A. C.
1928. The extent of the annual transplantation of plaice in the Limfjord and the yield resulting therefrom. *Rept. Dan. Biol. Sta.*, 1928, pp. 53-86.
- JUDAY, CHANCEY.
1924. Summary of quantitative investigations on Green Lake, Wisconsin. *Intern. Rev. der ges. Hydrob. und Hydrog.*, Vol. XII pp. 3-121.
- JUDAY, CHANCEY, AND SCHNEBERGER, EDWARD.
1930. Growth studies of game fish in Wisconsin lakes. Notes from the Biological Laboratory of the Wisconsin Geological and Natural History Survey, March, 1930.
- LEE, R. M.
1920. A review of the methods of age and growth determination in fishes by means of scales. *Min. of Agr. and Fish., Fish. Invest. Ser. II, Vol. IV, No. 2*, pp. 1-32.

MOHR, E. W.

1927. Bibliographie der Alters—und Wachstum Bestimmung bei Fischen. Jour. Cons., Vol. II, 1927, pp. 236-258.

VAN OOSTEN, J.

1923. The white fishes (*Coregonus clupeaformis*), a study of the scales of white fishes of known ages. Zoologica, N. Y., Vol. II, 1923, pp. 381-412, figs. 137-144.
1928. Life history of the lake herring (*Leucichthys artedi* Le Sueur) of Lake Huron as revealed by its scales, with a critique of the scale method. Bur. Fish., Dec., No. 1053.

PIROGNIKOFF, P. L.

1927. Materials concerning age and growth rate of rudd (*Rutilus rut. lacustris* Pallas) from the Lake Chani. Rep. Ichthy. Lab. in Siberia, Vol. II, No. 5, Krasnoyarsk, pp. 1-17. Russian; English summary.

POTTER, GEORGE E.

1925. Scales of the blue gill *Lepomis pallidus* (Mitchill). Amer. Micr. Soc., Vol. XL, No. 1, 1925.

RUGDE.

1923. Some notes from Norway. Salmon and Trout Mag., No. 34, 1923, pp. 333-337.

SCOTT, WILL.

1912. The regenerated scales of *Fundulus heteroclitus* Linne with a preliminary note on their formation. Proc. Ind. Acad. Sci., 1911, pp. 439-444.
1916. Report on the lakes of the Tippecanoe Basin (Indiana). Indiana Univer. Stud., Vol. III, Study No. 31, Bloomington, July, 1916.
1931. The Lakes of Northeastern Indiana. Pub. 107 Dept. of Cons. Indiana, pp. 55-142.

SCOTT, WILL, HILE, RALPH O. AND SPIETH, HERMAN T.

1928. A quantitative study of the bottom fauna, Lake Wawasee (Turkey Lake). Invest. of Ind. Lakes 1, Dept. Cons. Div. Fish and Game, 1928.

STRODTMANN, S., AND LANGHAMMER, L.

1925. Untersuchungen über die Scholle in der westlichen Ostsee. Berichte der D. W. Kom., N. F., Bd. I, No. XI, S. 305 u. ff. 1925.

TAYLOR, H. F.

1916. The structure and growth of the scales of the Squeteague and the pigfish as indicative of life history. Washington Bul. Bur. Fisheries, Vol. XXIV, 1914 (1916), 285-330, pls. 1-lix.

THOMSON, J. STUART.

1902. The periodic growth of scales in Gadidae and Pleuronectidae as an index of age. Jour. Mar. Biol. As., N. S. Vol. VI, pp. 373-375, pls. v.
1904. The periodic growth of scales in Gadidae as an index of age. Jour. Mar. Biol. As., N. S. Vol. VII, pp. 1-109, pls. i-viii.

TILLYARD, DR.

1921. Neuropteroid insects of the Hot Springs region, New Zealand, in relation to the problems of trout food. (Review in Salmon and Trout Magazine, No. 26, July, 1921.)

TJURIN, P. V.

1927. About the relation between the length of the fish and its weight. Rept. Sib. Sci. Sta. Fish., Vol. III, No. 3, 1927.

TODD, R. A.

1915. Report on the food of the plaice. Min. of Agr. and Fish. Ser. II, Vol. II, No. 3, London, 1912.

WRIGHT, STILLMAN.

1929. A preliminary report on the growth of the rock bass, *Ambloplites rupestris* (Rafinesque) in two lakes of northern Wisconsin. Trans. Wis. Acad. Sci., Arts and Letters, Vol. XXIV, 1929.

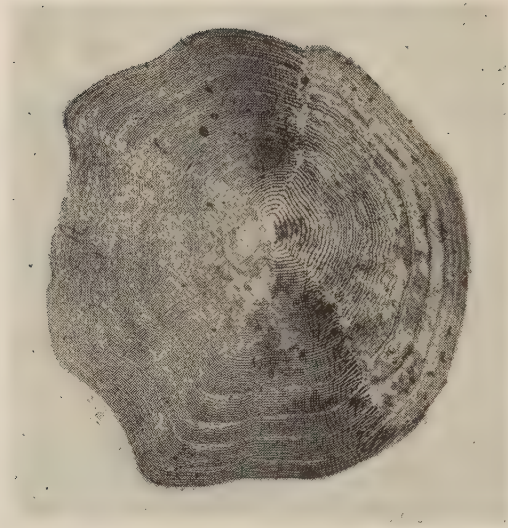


FIG. 1. Scale of Cisco. Age V. The growth area outside the fifth annulus indicates the growth of the sixth year. The fish was taken in the early winter.



FIG. 2. Scale of a Perch. Age I. A large growth is indicated in the second summer.



FIG. 3. Scale of Perch. Age VI. In this scale there is a dark band in the region of each annulus.



FIG. 4. Scale of Perch. Age IV.

Erratum: Captions for Figs. 3 and 4 are transposed.

APPENDIX

TABLE LXXXI.
TOTAL COLLECTIONS BY LAKES

LAKE	Blue Gill	Black Crappie	Long-eared Sunfish	Rock Bass	Large Mouth Black Bass	Small Mouth Black Bass	Silver Bass	Cisco	Pick-erel	Yellow Perch	Total
Syracuse.....	28		9	12	15					21	85
Wawasee.....	157	13	3	56	53	10			5	635	932
Papakeechee.....	3	2			4					1	10
Indian Village.....	47	15			2			62			126
Duley.....	53	8									61
Rider.....	24	6			1						31
Gordy.....	34							24			58
Hyndman.....	46							11			57
Dewart.....	45	7			1					6	59
Spear.....	1	2			3						6
Ridinger.....	3	3									6
Dan Kuhn.....	4										4
Big Barbee.....	20	10									30
Little Barbee.....	14	6									20
Tippecanoe.....	32	6		2	8		5			61	114
Little Chapman.....	25										25
Pike.....	5	5					1		1		12
Little Pike.....	9	12			1		3		7		32
Center.....	18	1									19
Winona.....	133	55	22	1	5				2	33	251
Silver.....	15	2									17
Total.....	716	153	34	71	93	10	9	97	15	757	1955

TABLE LXXXII.
LENGTH VALUES FOR CISCOES

LAKE	Date	YEAR CLASS					
		II	III	IV	V	VI	VII
Indian Village.....	11-26-28	25.7 (1)	30.4 (19)	31.9 (15)	32.7 (8)		33.3 (1)
Indian Village.....	7-21-29			32.4 (9)	33.4 (7)	33.4 (2)	
Gordy.....	-11-28						
Gordy.....	12- 1-28	26.4 (1)	29.7 (12)				
Gordy.....	7-23-29			31.8 (4)	37.7 (5)		39.4 (2)
Hyndman.....	8-12-29						
Hyndman.....	8-13-29	26.0 (1)	29.4 (3)	29.0 (5)		33.8 (2)	

TABLE LXXXIII.
LENGTH VALUES FOR PICKEREL

LAKE	Date	YEAR CLASS			
		III	IV	V	VI
Wawasee.....	7-18-26	30.3 (1)			
Wawasee.....	Apr., 1929		48.3 (1)	69.8 (2)	83.7 (1)
Pike.....	July, 1929		53.5 (1)		
Little Pike.....	July, Aug. 1929		45.7 (4)	45.0 (2)	54.6 (1)
Winona.....	July, 1929			67.8 (2)	

TABLE LXXXIV.
LENGTH VALUES FOR CRAPPIES

LAKE	Date	YEAR CLASS				
		II	III	IV	V	VI
Wawasee.....	7-25-27			20.6 (1)		
Wawasee.....	7- 5-29		18.3 (8)	19.4 (4)		
Indian Village.....	4-23-29			18.5 (8)	20.6 (3)	20.8 (1)
Indian Village.....	7-21-29		18.3 (3)			
Duley.....	4-23-29			18.0 (8)		
Rider.....	6-22-29		18.8 (6)			
Dewart.....			18.6 (7)			
Papakeechee.....	8- 8-26				20.8 (1)	20.3 (1)
Spear.....	7- 5-29		19.4 (2)			
Ridinger.....	6-20-29		19.0 (3)			
Big Barbee.....	7-15-29					
	7-29-29		18.4 (6)	19.3 (4)		
Little Barbee.....	7-13-29					
	7-30-29		17.7 (2)	18.5 (3)	20.0 (1)	
Tippecanoe.....	8-19-29					
	8-20-29		19.1 (2)	19.4 (4)		
Pike.....	July, 1929		19.8 (5)			
Little Pike.....	July, Aug., 1929			19.6 (6)	22.3 (4)	24.2 (2)
Center.....	7-21-29		18.7 (1)			
Winona.....	8-19-25	15.6 (1)				
Winona.....	July, Aug., 1929	14.9 (1)	18.3 (25)	21.2 (25)	22.8 (3)	
Silver.....			17.6 (2)			

TABLE LXXXV.
LENGTH VALUES FOR ROCK BASS

LAKE	Date	YEAR CLASS						
		I	II	III	IV	V	VI	VII
Syracuse.....	7- 7-27							
	7-18-27	5.9 (4)	10.0 (8)					
Wawasee.....	1926		14.2 (3)	17.0 (1)		22.7 (1)	23.3 (1)	
Wawasee.....	1927	5.6 (14)	10.5 (5)	14.5 (5)	17.8 (4)	18.4 (2)		23.4 (2)
Wawasee.....	1928	5.1 (5)	9.7 (1)	14.6 (1)	18.6 (4)	20.3 (1)		21.9 (1)
Wawasee.....	6-18-29							
	7- 1-29	5.1 (1)		17.2 (1)		21.8 (1)		
Tippecanoe.....	7-19-27			14.6 (1)		17.0 (1)		
Winona.....	7-31-26					17.0 (1)		

TABLE LXXXVI.
LENGTH VALUES FOR LONGEARED SUNFISH

YEAR CLASS	Syracuse 7-8-27	Wawasee 7-4-27	Wawasee 6-28-28	Winona 6-22-27 6-27-27	Winona 7-14-29
I	6.4 (1)				
II	9.2 (5)	7.5 (1)	7.5 (1)	7.3 (9)	7.7 (2)
III	10.0 (1)	11.1 (1)		8.1 (4)	11.2 (3)
IV	11.1 (1)			9.2 (2)	
V	12.4 (1)			9.4 (2)	

TABLE LXXXVII.
LENGTH VALUES FOR BLUE GILLS

LAKE	Date I	YEAR CLASS						
		I	II	III	IV	V	VI	VII
Syracuse.....	7- 3-26		11.2 (19)	17.3 (1)	17.1 (1)	17.6 (1)		
Syracuse.....	7- 8-27	5.1 (2)	9.7 (4)					
Wawasee.....	July, Aug., 1926		11.4 (77)	15.5 (14)	18.4 (14)	19.3 (7)	21.0 (1)	
Wawasee.....	July, 1927	5.3 (14)	9.8 (7)	20.2 (2)				
Wawasee.....	6-30-28			14. (1)	17.2 (2)	18.2 (6)	20.3 (1)	
Wawasee.....	Apr., 1929			15.6 (4)	16.6 (2)		19.7 (1)	
Wawasee.....	6-18-29							
Wawasee.....	7- 5-29			15.4 (2)	19.7 (1)	20.0 (1)		
Indian Village...	4-23-29			15.9 (3)	16.6 (28)	18.4 (3)		
Indian Village...	7-21-29			16.4 (9)	18.0 (3)	18.1 (1)		
Duley.....	4-23-29			15.8 (2)	16.3 (42)	16.9 (5)	17.6 (3)	19.1 (1)
Rider.....	6-20-29			15.8 (15)	16.9 (7)	18.7 (2)		
Gordy.....	11-26-28		14.5 (2)	16.7 (6)		18.3 (1)		
Gordy.....	7-23-29			15.9 (9)	17.5 (14)	18.7 (2)		
Hyndman.....	8-12-29							
Dewart.....	8-13-29			16.3 (33)	17.1 (11)	19.3 (2)		
Dewart.....	8-21-29							
Dewart.....	8-22-29			16.0 (35)	17.7 (10)			
Papakeechee....	8- 8-26					14.7 (2)	15.7 (1)	
Spear.....	7- 5-29			17.0 (1)				
Dan Kuhn.....	7-31-29			16.6 (2)	17.6 (2)			
Big Barbee.....	7-15-29							
Little Barbee....	7-29-29			15.8 (16)	17.8 (4)			
Little Barbee....	7-13-29							
Little Barbee....	7-30-29			15.6 (13)	17.6 (1)			
Tippecanoe.....	8-20-29							
Tippecanoe.....	8-21-29			15.9 (25)	18.0 (4)	18.6 (3)		
Ridinger.....	6-20-29			16.6 (3)				
Little Chapman..	7- 6-29			15.9 (12)	16.9 (13)			
Pike.....	July, 1929			15.9 (5)				
Little Pike.....	July, Aug., 1929			15.2 (6)	16.1 (3)			
Center.....	7- 2-29			15.6 (15)	16.5 (3)			
Winona.....	Aug., 1926	8.0 (1)	11.6 (3)					
Winona.....	July, 1929	8.7 (7)	11.6 (36)	15.0 (10)	17.5 (5)	19.1 (1)		
Winona.....	Aug., 1929	9.1 (2)	11.6 (44)	15.1 (13)	16.6 (11)			
Silver.....	8-10-29							
Silver.....	8-17-29			16.5 (14)	18.3 (1)			

TABLE LXXXVIII.
LENGTH VALUES FOR SMALL MOUTH BASS

YEAR CLASS	Wawasee July, 1926	Wawasee July, 1927
IV		27.4 (3)
V	27.3 (1)	
VI	33.7 (1)	31.8 (3)
VII		
VIII		41.0 (1)
IX	37.8 (1)	

TABLE LXXXIX.
LENGTH VALUES FOR LARGE MOUTH BASS

LAKE	Date	YEAR CLASS								
		O	I	II	III	IV	V	VII	VIII	XVI
Syracuse.....	7- 8-27	3.7 (1)	9.5 (13)	14.0 (1)						
Wawasee.....	7-1926						34.0 (1)		38.1 (1)	
Wawasee.....	7-1927		10.6 (4)		22.6 (3)	27.7 (1)	30.9 (6)			
Wawasee.....	6-19-28			14.8 (2)						
Wawasee.....	6-30-28		8.4 (5)	16.5 (1)						
Wawasee.....	7-14-28									
Wawasee.....	4-19-29					26.2 (19)	29.2 (2)			
Wawasee.....	6-18-29									
Indian Village	7- 5-29				25.1 (5)	27.4 (2)				
Indian Village	4-23-29					24.1 (1)				
Indian Village	7-23-29					24.1 (1)				
Rider.....							27.5 (1)			
Papakeechee...	1926					22.3 (1)			37.2 (1)	44.5 (1)
Papakeechee...	4-21-29								37.5 (1)	
Spear.....	4-21-29						27.0 (1)	31.4 (1)		
Spear.....	6-27-29					26.0 (1)				
Dewart.....	8-22-29					27.6 (1)				
Tippecanoe.....	7-19-27	3.5 (8)								
Little Pike.....	7-10-29					26.4 (1)				
Winona.....	7- 4-26					32.4 (1)				
Winona.....	7- 4-27							40.6 (1)		
Winona.....	7-26-27									
Winona.....	8-17-27						33.0 (1)		40.6 (1)	
Winona.....	7- 4-29						40.3 (1)			

TABLE XC.
LENGTH VALUES FOR PERCH

LAKE	Date	YEAR CLASS							
		O	I	II	III	IV	V	VI	
Syracuse.....	7- 3-26			14.7 (2)					
Syracuse.....	7- 2-27	4.2 (3)	9.6 (12)	11.1 (4)					
Wawasee.....	July, Aug., 1926		9.4 (5)	13.7 (25)	16.6 (27)	19.4 (9)	22.0 (3)		
Wawasee.....	7- 7-27	3.3 (5)	8.3 (27)	13.0 (11)					
Wawasee.....	7-14-27	3.4 (4)	8.8 (153)	13.4 (38)	16.8 (2)				
Wawasee.....	7-28-27		9.2 (36)	13.8 (18)					
Wawasee.....	8-17-27			14.9 (3)					
Wawasee.....	6-19-28								
Wawasee.....	6-20-28		7.4 (21)	11.7 (18)					
Wawasee.....	6-28-28		7.7 (5)	12.1 (14)	15.6 (2)	20.2 (2)			
Wawasee.....	6-30-28		7.9 (25)	12.0 (74)	19.1 (1)	20.4 (2)			
Wawasee.....	8-14-28	4.4 (10)	9.0 (26)						
Wawasee.....	10-10-28								
Wawasee.....	10-11-28			16.4 (7)	17.2 (3)	20.5 (2)			
Wawasee.....	7- 1-29		8.1 (38)	13.5 (18)	16.4 (1)				
Papakeechee...	8- 8-26							23.0 (1)	
Dewart.....	8-21-29								
Tippecanoe.....	8-22-29					26.4 (6)			
Tippecanoe.....	7-19-27	4.1 (29)	9.8 (32)						
Winona.....	8-14-25								
Winona.....	8-19-25	5.2 (15)	8.6 (10)	12.2 (8)					

TABLE XCI.
LENGTH VALUES FOR SILVER BASS

YEAR CLASS	Tippecanoe 8-20-29 8-21-29	Little Pike July, 1929	Pike 8-6-29
II	22.1 (2)		25.1 (1)
III	26.0 (3)	28.6 (3)	

TABLE XCII.
VALUES OF "K" FOR CISCOES

YEAR CLASS	Indian Village 7-21-29	Gordy 7-23-29	Hyndman 8-12-29, 8-13-29
II			1.56 (1)
III			1.79 (2)
IV	1.62 (16)	1.66 (4)	1.77 (5)
V	1.65 (2)	1.64 (5)	2.06 (1)
VI	1.60 (6)		1.90 (1)
VII		1.54 (2)	

TABLE XCIII.
VALUES OF "K" FOR CRAPPIES

LAKE	Date	YEAR CLASS				
		II	III	IV	V	VI
Wawasee.....	6- 8-29					
	7- 5-29		2.50 (9)	2.59 (4)		
Indian Village.....	4-23-29			2.66 (8)	2.62 (3)	3.19 (1)
Indian Village.....	7-21-29		2.47 (3)			
Duley.....	4-23-29			3.08 (8)		
Rider.....	6-20-29		2.29 (6)			
Dewart.....	8-21-29					
	8-22-29		2.58 (7)			
Ridinger.....	6-20-29		2.43 (3)			
Little Barbee.....	7-17-29					
	7-30-29		2.29 (2)	2.46 (3)		
Big Barbee.....	7-15-29					
	7-29-29		2.32 (6)	2.36 (4)		
Tippecanoe.....	8-19-29					
	8-20-29		2.67 (2)	2.44 (4)		
Pike.....	July, 1929		2.47 (5)			
Little Pike.....	July, Aug., 1929			2.17 (6)	1.93 (4)	2.26 (2)
Winona.....	July, 1929	2.27 (1)	2.33 (11)	2.41 (10)		
Winona.....	Aug., 1929		2.44 (14)	2.59 (9)	2.55 (3)	
Silver.....		2.46 (2)				

TABLE XCIV.
VALUES OF "K" FOR ROCK BASS

YEAR CLASS	Wawasee		
	July, 1926	July, 1927	YEAR June, 1928
II	3.54 (1)	3.14 (4)	
III	3.45 (4)	3.26 (5)	3.53 (1)
IV	3.53 (1)	3.32 (4)	3.18 (3)
V		3.77 (1)	3.53 (1)
VI	3.14 (2)		
VII		2.94 (3)	

TABLE XCV.
VALUES OF "K" FOR BLUE GILLS

LAKE	Date	YEAR CLASS					
		II	III	IV	V	VI	VII
Syracuse.....	7- 3-26	3.42 (19)	3.18 (1)	3.22 (1)	3.57 (1)		
Wawasee.....	July, 1926	3.27 (68)	3.37 (14)	3.33 (10)	3.39 (7)	3.53 (1)	
Wawasee.....	Apr., 1929		3.42 (1)	3.18 (4)			
Wawasee.....	6- 8-29						
	7- 9-29		4.06 (2)	3.81 (1)			
Indian Village.....	7-23-29		3.27 (3)	3.26 (28)	2.98 (3)		
Indian Village.....	7-21-29		3.04 (9)	3.11 (3)			
Duley.....	4-23-29		3.32 (2)	3.18 (42)	3.20 (5)	3.24 (3)	3.14 (1)
Rider.....	6-20-29		3.23 (15)	3.24 (7)	3.14 (2)		
Gordy.....	11-26-28	3.09 (1)	3.23 (1)		3.75 (1)		
Gordy.....	7-23-29		3.11 (9)	3.08 (14)	3.04 (2)		
Hyndman.....	8-12-29						
	8-13-29		3.44 (33)	3.23 (11)	3.14 (2)		
Dewart.....	8-21-29						
	8-22-29		3.15 (35)	2.90 (10)			
Ridinger.....	6-20-29		2.85 (3)				
Bib Barbee.....	7-15-29						
	7-29-29		3.22 (16)	3.15 (4)			
Little Barbee.....	7-17-29						
	7-30-29		3.13 (12)	3.12 (1)			
Tippecanoe.....	8-19-29						
	8-20-29		3.54 (25)	3.45 (4)	3.51 (3)		
Little Chapman.....	7- 8-27		3.08 (12)	3.16 (15)			
Pike.....	July, 1929		3.14 (5)				
Little Pike.....	Aug., 1929		3.44 (6)	3.12 (3)			
Center.....	7- 2-29		3.33 (15)	3.34 (3)			
Winona.....	June, July, 1929	2.62 (15)	3.07 (8)	2.72 (16)			
Winona.....	Aug., 1929	2.72 (41)	3.02 (13)	3.05 (11)			
Silver.....	8-10-29						
	8-17-29		3.02 (14)	2.66 (1)			

TABLE XCVI.
VALUES OF "K" FOR PERCH

YEAR CLASS	Winona 8-14, 19-25	Wawasee July, 1926	Wawasee 1927	Wawasee 1928	Wawasee 1929	Dewart 8-21, 22-29
0	1.34 (15)					
I	1.51 (10)		1.54 (216)	1.50 (77)	1.34 (38)	
II	1.56 (8)	1.69 (25)	1.70 (70)	1.63 (201)	1.30 (18)	
III		1.60 (27)				
IV		1.77 (9)				1.91 (6)
V		1.70 (3)				

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Fish Scales and Commercial Fisheries

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If a well grown specimen of any of the common varieties of fish were placed before twelve persons selected at random, and each person asked to record an estimate of its age, it is probable that the number of ages re-



Scale of Lake Huron herring. The three year marks are indicated by the black lines.

corded might be almost as great as the number of persons making estimates. All persons interested in fish and fishing are interested in the question of how fast a fish grows or how old some particular fish may be. Yet few have any but indefinite ideas on the subject, and among these few there is great disagreement.

It is nevertheless possible with many kinds of fish to determine individual ages with a high degree of accuracy. This is accomplished through a microscopic study of the structure of the scale. The accompanying photograph shows the typical structure of the scale of one of the common lake fishes, the

herring. The scale occupies the position it would have on the fish if the fish's head were pointed towards the left side of the page. The forward part (left in the picture) is imbedded in the fish's skin and is covered by the hinder portions of the preceding scales. The hinder part is exposed and is the part visible when the scale is on the fish.

It will be noticed that the scale is covered with roughly circular lines which are known as circuli. The distribution of these lines is not perfectly regular, but shows breaks at varying intervals. These breaks which extend entirely around the scales are the "year marks" by which the age is determined. They are known as annuli. The scale pictured here has three annuli, i.e., the fish has lived three full years and was in its fourth year when it was caught.

At the end of the summer season the growth of the fish slows down and during the winter ceases entirely or nearly so. Since the scale grows along with the fish, scale growth also comes to a standstill. When body and scale growth are resumed in the spring the first circuli of the new year are laid down without any reference to the position of the last circuli of the preceding summer. The result is a break in the regularity of the circuli — the year mark or annulus. An outstanding feature of the year mark may be noticed at the sides of the scale towards the hinder end. The last circuli of the summer do not pass completely around the scale but come to an end towards the back of the scale. The first spring

circuli do, on the contrary, pass entirely around the scale and thus cut across the ends of those of the preceding year.

If a fair sized scale is held up to the light the year marks can be seen. However some means of magnification is necessary if an accurate age determination is to be made. Considerable practice is necessary before scales can be read with confidence, and even a trained worker will ordinarily have to discard as unreadable the scales from about five per cent of the fish in his collection. Very old fish in particular are likely to have the later year marks so crowded that it is difficult or impossible to determine their exact ages. There is also variation in the clearness of marking in scales from different parts of the body of the same fish. Ordinarily the best scales are found about the middle of the fish just above or below the lateral lines. Certain species of fish have scales so difficult to read that they are worth little for growth study. An example is the common sucker.

It has been mentioned previously that the scale grows along with the fish. Since the number of scales does not increase as the fish becomes larger the growth of the scale is proportionate to that of the fish. This fact makes it possible not only to determine the age of the fish but also, by measuring the diameter of the scale within the various year marks, to calculate the length of the fish at the end of any particular year of life. Thus we may determine the rate of growth in the preceding summers.

Let us assume, for example that our three year old herring was twelve inches long and that the scale diameters when magnified measured: entire scale, 6 inches; scale within first year mark 3 inches, within the second $4\frac{1}{2}$ inches; and within the third, $5\frac{1}{2}$ inches. To determine how long the fish was at the end of the first year we calculate:

Length at end of first year = $\frac{3}{6} \times 12$, or 6 inches. Similarly we may determine that the fish was 9 inches long at the end of its second year, and 11 inches long at the end of its third year. It grew one inch in its fourth year before it was caught.

It is of interest to know that age marks occur also in the various bones of the fish. Some scientists have used bones instead of scales for the determination of age. Among the bones used have been those of the gill cover, vertebrae, fin rays, and especially the ear bones.

The use of scales for the determination of age was suggested as early as the 17th century by the Dutch scientist, van Leeuwenhoek. However there was no practical application of the reading of scales till in 1898 Prof. Hoffbauer, a German, published an article on the age determination of the carp. Since that time the method has been applied to many fishes in many localities. Perhaps the most extensive work has been done on the marine fishes of northern Europe.

There have also been numerous studies on age and growth of North American fishes, both marine and fresh water. Certain commercial fishes of the Great Lakes are included in the list. Canadian scientists have published articles on the growth of the cisco, yellow perch, and pike perch in Lake Erie and on the herring and certain of the chubs in Lake Ontario. Dr. Van Oosten of the United States Bureau of Fisheries has published a large paper on the growth of herring in Lake Huron. At the present time further age and growth studies by bureau investigators are in progress.

Age and growth investigations based on the examination of scales are of considerable value to the study of commercial fisheries. By this method it is possible to answer questions of the following type: At what age does a fish reach commercial size? At what age

Continued on Page 10

bled to make their preparations accordingly. The bureau hopes to establish in the near future a similar service on the Great Lakes, so that there may be available a sound scientific explanation for such phenomena as the present abundance of perch in Lake Erie, last year's general abundance of whitefish, and for periodic fluctuations in the lake fisheries in general.

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Fish Scales and Commercial Fisheries

Continued from Page 4

does it become mature? Are the fish in two given localities separate races or do their migrations lead to free mixing? How does pollution affect the fisheries by retarding growth? What percentage of the stock survives from year to year — is the commercial catch composed of fish of all ages or chiefly of young ones? If fishing has reduced the stock greatly, has faster growth resulted from the spraser population? As a specific illustration it may be pointed out that the herring of the Alpena and Saginaw bay regions are different stocks — their growth rates are not at all alike. Further, chemical pollution lowered the growth rate of the herring in Saginaw Bay causing a serious loss to commercial fishermen. Space permits the presentation of only one further example of the application of the scale method. In several important European and North American fisheries, investigators by following their age studies over a period of several years have arrived at the point of being able to predict fairly accurately the total catch for the coming season, and commercial fishermen were ena-

METHODS FOR THE INVESTIGATION OF THE STATISTICS OF THE COMMERCIAL FISHERIES OF THE GREAT LAKES*

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The Great Lakes are the chief source of supply of freshwater fish in the United States. For this reason they are subjected to an increasingly heavy fishery, and for the same reason the maintenance of their waters at the point of maximum production efficiency is of primary importance. Just how to determine and maintain that point of maximum efficiency is the chief problem confronting the fisheries today.

Past experiences have given repeated examples of the dire results which follow upon the ruthless exploitation of even the seemingly inexhaustible fisheries. The sturgeon has passed from the status of being a nuisance to that of being a rarity; the cisco of Lake Erie is no longer of commercial importance; and today in certain waters the chub bids fair to suffer a like fate. Still other forms, while not approaching extinction, show signs of rather severe depletion.

The rehabilitation of a ruined fishery is at its best a laborious, troublesome, and drawn out task. Nor is there any certainty that a commercially extinct species can by any measures ever be returned to its former condition of abundance. The sane method of protection of fisheries consists in the prevention, not the remedying of disaster. The catastrophes which have overtaken certain fisheries in the past might have been averted had their impending occurrence been realized early and precautionary measures adopted.

The future of the Great Lakes fisheries demands the prevention of disasters such as have occurred in the past. If the commercial extinction of a species is to be avoided there must be some means of measuring its changes in abundance, of detecting any dangerous depletion of the stock. For this purpose an accurate and comprehensive system of fisheries statistics is necessary.

In the past those persons who are interested in the welfare of the Great Lake fisheries have found the lack of adequate and accurate statistical data a severe handicap in their efforts towards the conservation and maintenance of the stock. It is only within recent years that the states along the Great Lakes have made any move towards a detailed and systematic collection of data pertaining to their commercial fisheries. In some instances these moves have unfortunately

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proved abortive and few data of real value have been accrued. In others the state officials have prosecuted the collection of statistics with such diligence that the data they have collected represent, for practical purposes, a complete record of the commercial fishing operations in the waters under their jurisdiction.

The state of Michigan has been a pioneer among the Great Lakes states in the matter of the systematic collection of fisheries statistics. Since September, 1927, they have required the submission of a monthly report from each licensed fisherman. During 1927 and 1928 the set of returns was by no means complete. Further, the inexperience of the fishermen in filling out the reports was such that many of them were of little use for statistical study. It was also found necessary in the earlier stages of the work to make certain changes in the arrangement and content of the original report sheets. Since the beginning of 1929, however, there has been a rigid enforcement of the rule which requires the regular submission of reports, and reports which were not made out properly were returned to their senders for correction. As a result, for the past four and one-half years there has been accumulated a highly reliable mass of information on the statistics of the commercial fisheries of the state of Michigan. These data cover the greatest period of time and the greatest diversity of gear and of fishing conditions of any similar materials available with respect to the Great Lakes fisheries. For these reasons they are being used as the basis of the Bureau's present investigation of the statistics of the Great Lakes fisheries. It is hoped that their study may lead to the development and perfection of standardized methods applicable to all Great Lakes fisheries, and that ultimately all the Great Lakes states will adopt a uniform method for the collection and analysis of much needed data relative to the statistics of their fisheries. The bureau acknowledges its indebtedness to the Michigan Department of Conservation for this invaluable source of material, and recognizes particularly the untiring efforts of the Honorable William H. Loutit, Chairman of the Department of Conservation, and Mr. Fred Westerman, in charge of the Fish Division, who have made such an efficient collection of data possible.

The monthly report submitted by each licensed Michigan fisherman contains a daily record of the kind and amount of gear lifted, the length of time over which it has fished, the location of the fishing grounds, and the catch in pounds for each species. To avoid confusion it is required that a separate report be filed for each type of gear fished.

For purposes of analysis of the statistical data the various lakes under the jurisdiction of the State of Michigan have been divided into districts. There are eleven districts in Lake Michigan, seven in Superior, six in Huron, one in St. Clair, and one in Erie. It has been attempted to make these districts the most natural divisions

of the fishing grounds possible. Thus it is possible to study the various areas within the lake separately, and a simple summation provides the data for the entire lake.

The work of actual analysis of the statistics has only begun. Up to the present time the chief concern has been the development of methods of procedure. The nature of the Great Lakes fisheries is such that many of the methods ordinarily used in the treatment of fisheries statistics are not applicable here. The marine fisheries that have been subjected to detailed statistical studies have been unit fisheries, that is, fisheries in which the catch is comprised of a single important species. In the Great Lakes the hook fishery for trout is the only unit fishery. In other types of gear the catch is regularly composed of several important species, and each species is taken regularly by several types of gear. These circumstances introduce a complexity which requires the development of special methods adapted to the proper study of the special problems which the Great Lakes fisheries statistics present. It is the purpose of this article to call attention to certain of the peculiarities and problems connected with the study of the Great Lakes statistics, and to describe the methods by which it is proposed to obtain information bearing on them. The nature of these problems will appear in the following discussions of the methods of analysis of yield, effort, and yield in relation to effort. Almost all the illustrations will be drawn from District I of Lake Huron. This district comprises the most northerly portion of the aforementioned lake, and its limits are defined as follows: Entire area west of a line drawn from Drummond Island across the lake to and including Rogers City, Presque Isle County.

Yield: The yield of the fishery is considered from the following standpoints:

A. Annual yield:

- (1) Total annual production by species (Table 1).
- (2) Total annual production by gear (Table 2).
- (3) Total annual production by species for each type of gear. (See Table 3, production of 4½" mesh gill net, as an example).

B. Yield within a single year:

- (1) Total monthly production by species (Table 4).
- (2) Monthly production by species for each type of gear. (See Table 5, monthly production of pound nets, as an example).

C. Yield for a single species:

- (1) Annual catch. (See Table 6, annual whitefish catch, as an example).
- (2) Monthly catch in each type of gear. (See Table 7, monthly whitefish catch, as an example).

In so far as yield in the above illustrations is concerned, our method does not differ from those employed elsewhere.

Effort: It is in relation to the study of fishing effort that the

special nature of the Great Lakes fisheries becomes most apparent. The fishing of the $2\frac{3}{4}$ " mesh gill net will serve well as an illustration. With this type of gear there exist two distinct fisheries—the shallow water fishery for perch, herring, menominees, and other shoal water fish, and the deep water fishery for chubs. The two fisheries do not overlap. A gang of $2\frac{3}{4}$ " mesh nets set in shallow water will take shallow water forms but will capture no chubs. The same nets set in deep water will take chubs (and small trout) but will capture none of the shallow water forms. It is obvious that a tabulation of the fishing effort exerted for the capture of chubs should not include the effort represented by the lifts of $2\frac{3}{4}$ " mesh gill nets which were set in shallow water. Nor should the effort listed for the capture of perch, herring, and other shallow water forms include the effort represented by the $2\frac{3}{4}$ " mesh gill nets which were fished in deep water, and which took only chubs and small trout. In spite of the identity of type of gear used the shallow water and deep water fisheries with the small-mesh gill net are completely distinct and must be considered separately. Almost every type of gear offers similar examples of efforts which have been exerted in quite different directions, and thus represent distinct fisheries.

It can be seen that a discriminating analysis of the Great Lakes fisheries statistics requires a separate listing of the effort exerted for the capture of each species. To achieve this end we have made the following definition of effective effort: *Effective fishing effort with respect to a given species is effort which has resulted in the capture of any quantity of that species.* The use of effective fishing effort is intended as a means of distributing effort according to the direction in which it has been exerted, and not as an elimination of fishing failures. As a matter of fact the original report sheets offer few examples of a failure of any gear to take at least a few of a species which is ordinarily to be found on the grounds upon which that gear was set. A decrease in the general population is reflected in generally smaller catches rather than in a notable increase in the number of failures. On the whole the tendency towards shoaling in the Great Lakes fishes is not sufficiently great to make the fishery a hit and miss affair. It is this fact which makes the use of effective effort valid.

The study of effort in a unit fishery is a comparatively simple affair, for here *effective* and *total* effort are identical quantities. For example, in most regions of the Great Lakes every hook lifted can be considered to have fished for trout. As an example of a similar situation in the marine fisheries we may consider the trawl fishery for plaice, where it is certain that every hour's trawling actually represents effort for the capture of plaice. It should be mentioned, however, that a study of effort in pl fishing would hardly in-

clude the effort represented by the haul of trawls used in the herring fishery.

For an illustration of the tabulation of the effort of a single type of fishing gear over the period of a year, consult Table 8. To show the significance of the data consider the month of May. During this month there were 310 pound net lifts (total effort). Trout occurred in 288 of these lifts, whitefish in 300, herring in three, and yellow pike in 17 (effective efforts). Such a separation is justifiable as the nature of the catch of a pound net depends quite closely upon the locality in which it was set. A pound net in one locality may take large catches of whitefish and no herring. The same net, if it were moved to another location, might take large catches of herring and no whitefish.

In many instances the study of fishing intensity and of changes in abundance requires the introduction of the time element into the analysis of the data relative to fishing effort. As an illustration of this point consider the relative fishing efforts of two lifts 25,000 feet of gill net, the first of which has been in the water two days while the second has been set four days. On the basis of the amount of gear lifted they represent equal amounts of fishing effort. Actually the nets of the second lift have fished twice as much as those of the first. Within a single geographical area the average amount of time over which a particular type of gear is allowed to fish before it is lifted does not vary greatly from year to year. There is, however, within the same geographic region, a considerable variation in the fishing time of certain types of gear from one time of the year to another. Further, different regions show consistent annual and seasonal differences in the fishing time of the same type of gears, and different types of gear have different characteristic fishing times (See bottom of Table 10). Because of these facts it is necessary that time be considered in the study of seasonal changes in abundance within an area and in the comparison of two separated areas. Two examples should be sufficient illustration.

To show the importance of time in the study of seasonal changes in abundance, assume that it is desired to compare the abundance of trout on the gill net fishing grounds of District I, Lake Huron, in the months of April and October, 1930. The catch in April was 11.0 pounds for each 1,000 feet of large mesh net lifted. In October the catch was 34.8 pounds for each lift of 1,000 feet. From these figures it might be inferred that trout were approximately 3.2 times as abundant in October as in April. If, however, the effort is considered in terms of the action of 1,000 feet of net over the period of one day the production figures become: April—3.0 pounds; October—19.1 pounds, and the data indicate that on the gill net grounds trout were 6.4, not 3.2 times more abundant in October than in April. The discrepancy finds its origin in the fact

that in April gill nets fished for trout were in the water approximately four days before lifting, and in October only two days.

Similarly, time is of importance in comparisons which involve geographically separated areas as may be seen in the comparison of the fishing efficiency of pound nets in Districts I and III, Lake Huron, during the 1930 season. The average lifts in pounds of pound nets were: District I—151 pounds; District III—314 pounds. From these data it would appear that the District III pound nets were 2.08 times as effective as those of District I. The actual catches of pound nets per night of fishing were: District I—55.9 pounds; District III—152.3 pounds. Thus it may be seen that the District III pound nets were 2.72, not 2.08, times as effective as those of District I. The reason for the difference is that the fishing time of pound nets in District I was 2.7 days while in District III it was 2.1 days.

The time element does not enter into the study of the seine fishery, and it must remain an undetermined factor in the insignificant hand line and dip net fisheries.

In connection with the study of fishing effort the following terms have been defined:

1. **Net lift:** The effort represented by the lift of one net. (Trap, pound, fyke, hoop).
2. **Net night:** The fishing effort of one net over the period of one day. (Trap, pound, fyke, hoop). The number of nights out is taken as the measure of time.
3. **Foot lift:** The effort represented by the lift of one foot of gill net.
4. **Foot night:** The fishing effort of one foot of gill net over the period of one day. The actual units used are (3) 1000 foot lifts and (4) 1000 foot nights.
5. **Hook lift:** The effort represented by the lift of one hook.
6. **Hook night:** The fishing effort of one hook over the period of one day. The actual units used are (5) 1000 hook lifts and (6) 1000 hook nights.
7. **Rod-haul:** The effort represented by the haul of one rod of seine. The unit used is 100 rod hauls.

Fishing effort measured without reference to fishing time, and fishing effort in which the time element has been introduced are both real and reliable quantities. They differ with respect to the point of view from which the fishery is being considered. The former measure of effort represents the actual amount of energy which the fisherman exerts. The latter is a measure of the actual intensity of fishing. For the purpose of distinguishing the two types of effort we define that effort which does not consider the time element merely as *fishing effort* and that effort which takes time into consideration as *fishing intensity*. In the seine fishery, of course, the two types are identical. Tables 9 and 10 show total fishing effort and total fishing intensity in District I for each of the years 1929-1932.

The yield in relation to the amount of fishing can be expressed as *yield per unit effort* or as *yield per unit intensity*. The former measures the return to the fisherman per unit amount of labor expended. The latter is a measure of the abundance of fish on the fishing grounds. Since effort can be considered on the basis of total effort and effective effort (the same applies to intensity) the unit yield can be expressed by any one of four quantities. As an illustration consider the yield of trout in relation to the amount of fishing in the year 1931 (Table 11). With respect to trap nets, for example, the data signify as follows: (1) In trap nets which caught trout the average lift was 22.41 pounds of trout (yield per unit effective effort). (2) For every trap net lifted in District I in 1931 there were captured 7.86 pounds of trout (yield per unit total effort). (3) Each net which captured trout took an average of 5.77 pounds of that fish each night it fished (yield per unit effective intensity). (4) For a day's fishing of every trap net in the district in 1931 there were captured 1.56 pounds of trout (yield per unit total intensity). The implications with respect to the other types of gear are similar. The units of effort and intensity have already been defined (p. 10).

For a second example of the tabulation of the different types of unit yield consult Table 12, which shows a tabulation of yield in relation to the amount of fishing for the various species taken in the pound nets of District I, 1932. The sums of the separate yields, catch per lift and catch per night as based on total fishing gear, represent the average catch in pounds per lift and average catch in pounds per night (all species) for all pound nets of the district (last column, Table 12). These average catches per unit effort and per unit intensity are shown in Table 13 for all types of gear over the four-year period (1929-1932).

The study of the variation in unit yield of the trap nets (see Table 13) furnishes an excellent example of the importance of listing effort and intensity both as total quantities and as to their effective distribution with respect to the different species. It will be noticed that in 1930 the average lift in pounds for trap nets was nearly double that of the preceding year. In 1931 the average lift increased still more, but fell off considerably in 1932. The changes in yield per unit intensity followed a similar trend. From our acquaintance with the fishery we know that these great annual fluctuations in the average yield of trap nets do not represent correspondingly large changes in abundance of fish on the fishing grounds, but that they resulted from the introduction into the fishery of a new type of trap net, the deep trap, or "sub." Prior to 1930 practically all trap nets fished in northern Lake Huron were "shallow traps." Their catch consisted chiefly of suckers, yellow pike, perch, and other shallow water species. In 1930, however, the deep trap or "sub" came into general use for the capture of white-

fish (deep traps ordinarily take small but important catches of trout). The introduction of the deep trap net meant the establishment of a new fishery, a fishery quite different from the shallow trap net fishery. Since the fisherman's original reports do not distinguish between deep and shallow traps it was found necessary in order to separate the two fisheries to turn to the study of the effective fishing efforts of the trap nets.

The consideration of the fishing efforts of trap nets was centered on the most important species of each type. In Huron, District I these are in the shallow trap the sucker, and in the deep trap the whitefish and the trout. Table 14 shows the percentage of trap nets lifted which were effective in the taking of whitefish, suckers, and trout in each of the years, 1929 to 1932. It will be seen that the sum of the percentages for whitefish and suckers in each year approximates 100 per cent quite closely. Since in 1929, when deep trap nets were not fished whitefish were taken in approximately two per cent of the trap nets, an estimate that the percentage of deep trap nets in the total trap net lifts is two less than the listed effective percentage for whitefish probably varies insignificantly from the truth. In the computation of average lifts for the two types of gear all whitefish and trout are considered to come from deep trap nets, and the catches of species other than the aforementioned two are credited to shallow traps. The examination of individual fishing reports justifies the procedure.

The selection of units of effort and intensity hinged upon the question of convenience in treating the data of the original report sheets. As defined they do not represent equivalent amounts of labor on the part of the fishermen. An understanding of the relative effectiveness of the various types of gear as represented by returns to the fisherman for his labor can be obtained better from a comparison of their catches for a typical day's fishing. A lift of 30,000 feet of gill nets is considered a reasonable day's work. It is estimated that lifts of seven deep traps, eleven shallow traps, ten pound nets, or 2,400 hooks correspond approximately to the above mentioned gill net lift. On the basis of the above assumptions the daily yields for the various types of gear have been computed. (Table 15). The table shows that from the standpoint of daily yield in pounds the $4\frac{1}{2}$ " mesh gill net is the least effective gear and the pound net the most effective. The deep trap gave excellent yields during the year of its introduction. The yield fell off slightly during the second year and suffered a tremendous decrease during the third. Of course the various types of gear vary as to the species composition of the catch and consequently as to the value per pound of the fish taken. It is, however, beyond the scope of this investigation to enter into a discussion of prices, marketing, or the general economic problems of the fisheries.

Table 16 shows the nature of the annual summary which is pre-

pared for each important species in each fishing district. In view of the preceding discussion no further explanations of the contents of the table should be necessary.

There will be offered a single example of the application of statistical data to a practical fisheries problem. The year 1928 saw the introduction into Lake Huron of the deep trap or "sub" for the capture of whitefish.¹ In 1930 the deep trap had become fairly common, and since that time there has been a regular increase in its use. The efficiency of this type of gear is so great that there have arisen grave fears that its continued use may result in a serious, even disastrous depletion of the whitefish stock. Table 17 shows the position of the deep trap in the whitefish fishery of northern Lake Huron over the period 1929-1932. These data show that the changes in total whitefish production in District I were in large measure, although by no means entirely, dependent upon the changes in the production of the deep trap nets. The catch per unit effort was greatest in the year deep trap nets first became common, decreased slightly the following year, and fell off markedly during the third year of their use. Simultaneous with the great decrease in the catch per unit effort there occurred a falling off in the number of deep trap nets fished.

No definite conclusions can be made as to the effect of deep trap nets on the fishery for whitefish until the statistics of the catch have been analyzed for the entire lake. The 1933 statistics should offer further important data. In general the spread of the deep trap in Lake Huron has been from north to south. There is some reason for belief that the introduction of this gear into a new locality is followed by two years of good fishing, while the third season is at least a partial failure. The catch statistics should show whether this gear does actually accomplish such a rapid and severe depletion of local whitefish populations.

SUMMARY

There has been presented a description of the methods which are being developed for the treatment of the statistics of the commercial fisheries of the Great Lakes.

The tabulation of the yield in geographic districts by gear and by species for each year and each month offers no innovations on the methods ordinarily employed for the study of commercial fisheries statistics.

The existence in the Great Lakes of distinct and separate fisheries which employ identical types of gear, and the seasonal and geographic variations in the average fishing time of the various types of gear have made nec-

¹For descriptions of the deep trap net and discussion of the problems which have resulted from its use consult: Jobes, Frank W.—Deep trap nets on Lakes Huron and Michigan. *The Fisherman*, Vol. I, No. 3, February, 1932, Grand Haven, Michigan. Westerman, Fred A.—The deep water trap net and its relation to the Great Lakes Fisheries. *Trans. Am. Fish. Soc.*, 1932, pp. 64-71.

essary certain improvements on the common method of describing fishing effort as the total amount of gear lifted, total number of seine hauls, total trawling hours, etc. In the study of fishing effort the following terms are defined:

I. Fishing effort

- a. The fishing effort in a day's lift is the amount of gear lifted (in terms of units which have been defined on pages 295 and 296.
- b. The total fishing effort with respect to a particular type of gear and over a specified period of time is the sum of the separate lifts.
- c. The effective fishing effort with respect to a particular species, a particular type of gear, and over a specified period of time is that part of the total fishing effort which has resulted in the capture of any quantity of that species.

II. Fishing intensity

- a. The fishing intensity in a day's lift is the product, fishing effort x fishing time (nights out). Special intensity units have been defined on pages 295 and 296.
- b. The total fishing intensity with respect to a particular type of gear and over a specified period of time is the sum of the products, effort x fishing time, as computed separately for each day's lift.
- c. The effective fishing intensity with respect to a particular species, a particular type of gear, and over a specified period of time is that part of the total fishing intensity which has resulted in the capture of any quantity of that species.

There have been offered examples to show the applications of the methods to the study of seasonal and annual fluctuations in yield and abundance and to the study of fishing gears, their seasonal and annual changes in yield and catch composition, and the relative importance of each type of gear in the general fishery.

TABLE 1

Lake Huron, District 1. Catch in Pounds of Each of the More Important Species in the Commercial Fishery, 1929-1932

Year	Trout	Whitefish	Chubs	Suckers	Menominee	Yellow Pike	Perch	Herring	Miscellaneous	Total
1929	374,328	385,280	241,005	234,987	48,813	14,914	19,525	28,135	61,723	1,408,710
1930	475,444	692,735	352,769	178,428	41,543	25,054	19,389	22,611	112,312	1,920,285
1931	542,161	941,768	420,335	372,119	33,154	36,506	21,753	11,902	135,582	2,515,280
1932	511,101	593,999	443,302	568,872	18,167	40,832	24,443	8,173	74,143	2,283,032
Total	1,903,034	2,613,782	1,457,411	1,354,406	141,677	117,306	85,110	70,821	383,760	8,127,307
Per ct.	23.42	32.16	17.93	16.66	1.74	1.44	1.05	0.87	4.72	

TABLE 2

Lake Huron, District 1. Catch in pounds (all species) for each type of commercial fishing gear, 1929-1932

Year	2¾" Gill Net	4½" Gill Net	Trap	Pound	Hook	Fyke	Hoop	Seine	Gear Unknown	Total
1932	470,478	364,316	865,907	415,118	123,122				44,096	2,283,032
1931	465,992	500,187	881,251	445,413	112,929	1,485		26,550	81,473	2,515,280
1930	414,598	444,209	520,146	443,638	52,764		3,219		41,711	1,920,285
1929	300,359	512,787	269,404	265,265	47,155				13,740	1,408,710
Total	1,651,422	1,821,499	2,536,708	1,569,434	335,970	1,485	3,219	26,550	181,020	8,127,307
Per ct.	20.32	22.41	31.21	19.31	4.13	0.02	0.04	0.33	2.23	

TABLE 3

Lake Huron, District 1. Catch in pounds in 4½" mesh gill nets, 1929-1932
Listed according to species

Year	Trout	White- fish	Chub	Sucker	Meno- minee	Yellow pike	Perch	Herring	Miscel- laneous	Total
1929	260,934	213,371	145	26,831	9,115	325	5		2,061	512,787
1930	275,139	146,925	5	8,401	1,888	1,397	191	38	10,918	444,209
1931	286,594	207,816		1,617	533	157	618		2,852	500,187
1932	255,660	104,824	178	1,143	1,412	250			849	364,316
Total	1,078,327	672,936	328	37,992	12,948	2,129	814	38	15,987	1,821,499
Per ct.	59.20	36.94	0.02	2.09	0.71	0.12	0.04	0.00	0.88	

TABLE 4

Lake Huron, District 1, 1931. Monthly catch, in pounds, of all types of gear combined
for each of the more important species in the commercial fishery

Month	Trout	Whitefish	Chub	Sucker	Menominee	Yellow Pike	Perch	Herring	Misc.	Total
January	61,868	390	5,235	799	174		93	689	409	69,657
Feb'ary	18,228	220	6,568	5,520	1,267		260	855	916	33,834
March	11,921	297	9,273	4,329	1,520		62	259	2,520	30,181
April	50,627	54,719	22,133	13,411	1,347			2,192	10,675	155,104
May	55,046	146,823	41,113	42,245	4,046	75		849	13,987	304,184
June	53,252	293,630	36,038	102,823	2,825	2,408	1,206	1,009	19,735	512,926
July	43,152	138,733	66,327	56,335	6,135	2,689	663	1,218	3,768	319,020
August	53,006	126,635	55,316	50,395	4,684	15,208	2,943	272	19,428	327,887
Septem'r	52,006	86,640	66,822	35,226	579	12,492	6,795	553	34,127	295,240
October	91,862	33,375	54,693	13,116	2,822	3,175	2,455	2,056	24,428	227,982
Novem'r	31,496	41,801	36,886	12,337	5,813	452	6,008	906	5,231	140,924
Decem'r	19,703	18,505	19,931	35,583	1,942	7	1,268	1,044	358	98,341
Total	542,161	941,768	420,335	372,119	33,154	36,506	21,753	11,902	135,582	2,515,280
Percent.	21.55	37.44	16.71	14.79	1.32	1.45	0.86	0.47	5.39	

TABLE 5

Lake Huron, District 1, 1931. Monthly catch (in pounds) of pound nets, listed according
to species

Month	Trout	Whitefish	Chub	Sucker	Menominee	Yellow Pike	Perch	Herring	Misc.	Total
January										
February	45							23		68
March	80	55								135
April										
May	7,937	19,150			18	65		15	165	27,350
June	20,712	142,159		671	1,161	104			2,800	167,607
July	12,164	63,585		663	11	205		455	6	77,089
August	4,464	30,665		3,872	14	985	412	177	2,304	42,893
Septem'r	6,426	34,272	30	2,081	16	2,989	22	362	7,967	54,165
October	12,870	23,223		286	86	787	40	1,914	1,479	40,685
Novem'r	4,522	29,688		3	149	59				34,421
December	651	349								1,000
Total	69,871	343,146	30	7,576	1,455	5,194	474	2,946	14,721	445,413
Percent.	15.69	77.04	0.01	1.70	0.33	1.17	0.11	0.66	3.31	

TABLE 6

Lake Huron, District 1. Annual catch of whitefish (in pounds) in each type of effective
fishing gear, 1929-1932

Year	2¾-Inch Gill Net	4½-Inch Gill Net	Trap	Pound	Gear Unknown	Total
1929		213,371	1,332	170,466	111	385,280
1930	957	146,925	203,903	336,736	4,214	692,735
1931		207,816	367,001	343,146	23,805	941,768
1932		104,824	160,962	313,500	14,713	593,999
Total	957	672,936	733,198	1,163,848	42,843	2,613,782
Percentage	0.04	25.75	28.05	44.53	1.64	

TABLE 7

Lake Huron, District 1, 1931. Monthly catch of whitefish (in pounds) for each effective type of fishing gear

1931	4½-Inch Gill Net	Trap	Pound	No Gear Listed	Total	Percentage
January	390				390	0.03
February	220				220	0.02
March	125		55	117	297	0.03
April	41,726	12,993			54,719	5.81
May	57,561	70,112	19,150		146,823	15.59
June	31,201	104,943	142,159	15,327	293,630	31.18
July	18,932	51,202	63,585	5,014	138,733	14.73
August	24,560	71,203	30,665	207	126,635	13.45
September	7,936	42,455	34,272	1,977	86,640	9.20
October	225	9,927	23,223		33,375	3.54
November	6,847	4,103	29,688	1,163	41,801	4.44
December	18,093	63	349		18,505	1.96
Total	207,816	367,001	343,146	23,805	941,768	
Percentage	22.07	38.97	36.44	2.53		

TABLE 8

Lake Huron, District 1, 1931. Number of pound nets lifted during each month and the number of lifts which contained catches of each of the important species

1931	Trout	Whitefish	Chub	Herring	Sucker	Pike	Perch	Total Lift In Month
January								
February	2			10				10
March	27	27						27
April								
May	288	300		3		17		310
June	798	858			10	58		853
July	633	685		12	21	55		696
August	351	477		12	54	106	17	490
September	461	689	6	82	179	349	4	691
October	436	533		81	5	211	2	658
November	168	220			2	20		230
December	20	16						20
Total	3,184	3,805	6	200	271	816	23	3,990
Percentage Effective	79.80	95.36	0.15	5.00	6.79	20.45	0.58	

TABLE 9

Lake Huron, District 1. Total fishing effort (gear lifted) for each type of gear for each year, 1929-1932¹

Year	2¾" Gill Net	4½" Gill Net	Trap	Pound	Fyke	Hoop	Hook	Seine
1929	14,590	24,799	5,162	2,567			146	
1930	13,981	18,747	5,051	2,939		23	258	
1931	14,856	26,410	7,663	3,990	51		427	17
1932	16,378	20,631	9,764	4,060			488	

¹Units of effort are: gill nets, 1,000 ft. lifts; trap, pound, fyke, hoop—1 net lift; hooks, 1,000 hook lifts; seine, 100 rod hauls.

TABLE 10

Lake Huron, District 1. Total fishing intensity¹ for each type of gear for each year, 1929-1932. Below, the average fishing time (in days) for each type of gear

Year	2¾" Gill Net	4½" Gill Net	Trap	Pound	Fyke	Hoop	Hook	Seine
1929	92,889	87,591	34,463	7,676			541	
1930	82,248	69,813	26,825	7,932		161	956	
1931	89,026	86,829	38,550	10,435	227		1,701	17
1932	98,120	73,449	44,926	10,910			1,991	
Average Fishing Time	6.1	3.5	5.2	2.7	4.5	7.0	3.9	

¹Units of fishing intensity: gill nets, 1,000 ft. nights; trap, pound, fyke, hoop—1 net night; hooks, 1,000 hook nights; seine, 100 rod hauls.

TABLE 11

Lake Huron, District 1, 1931. Trout fishery: Yield per unit fishing effort and per unit fishing intensity expressed for each type of gear with respect to both effective and total effort and intensity. Below, total catch in pounds in each type of gear

	2¾" Gill Net	4½" Gill Net	Trap	Pound	Hook
Catch per Lift—Effective Gear	0.60	11.09	22.41	21.94	263.80
Catch per Lift—Total Gear	0.48	10.85	7.86	17.51	263.80
Catch per Night—Effective Gear	0.10	3.36	5.77	8.62	66.22
Catch per Night—Total Gear	0.08	3.30	1.56	6.70	66.22
Total Catch in Pounds	7,066	286,594	60,236	69,871	112,644

TABLE 12

Lake Huron, District 1, 1932, Pound net fishery: Catch per unit effort and per unit intensity for each of the important species. Values are given with respect to both effort and total effort and intensity. Below, catch in pounds of each of the important species

	Trout	Whitefish	Herring	Sucker	Yellow Pike	Miscellaneous	Total
Catch per Lift—Effective Gear	25.10	79.27	8.07	35.20	7.17		
Catch per Lift—Total Gear	20.02	77.22	0.77	2.22	1.28	0.88	102.39
Catch per Night—Effective Gear	9.15	29.62	3.17	11.32	2.30		
Catch per Night—Total Gear	7.39	28.74	0.29	0.83	0.48	0.32	38.05
Catch in Pounds	80,651	313,500	3,143	9,010	5,206	3,608	415,118

TABLE 13

Lake Huron, District 1. Catch in pounds per unit effort and per unit intensity for each type of gear used in the commercial fishery, 1929-1932. These catches are based on all gear fished and on the combined catches of all species taken in a particular type of gear

	2¾" Gill Net	4½" Gill Net	Trap	Pound	Fyke	Hoop	Hook	Seine
1929 Catch per Unit Effort	20.59	20.68	52.19	103.34			322.98	
1929 Catch per Unit Intensity	3.23	5.85	7.82	34.56			87.16	
1930 Catch per Unit Effort	29.65	23.69	102.98	150.95		139.96	204.51	
1930 Catch per Unit Intensity	5.04	6.36	19.39	55.93		19.99	55.19	
1931 Catch per Unit Effort	31.37	18.94	115.01	111.63	28.11		264.47	1,580.35
1931 Catch per Unit Intensity	5.23	5.76	22.86	42.68	6.54		66.39	
1932 Catch per Unit Effort	28.73	17.66	88.71	102.39			252.30	
1932 Catch per Unit Intensity	4.80	4.96	19.27	38.05			61.84	

TABLE 14

Lake Huron, District 1. Trap net fishery: Changes in the percentage effort exerted for the capture of whitefish, suckers, and trout, 1929-1932

	1929	1930	1931	1932
Percentage Trap Nets Taking Whitefish	2.38	29.80	36.97	20.17
Percentage Trap Nets Taking Suckers	96.24	73.25	64.92	81.06
Percentage Trap Nets Taking Trout	4.22	23.84	35.08	17.39

TABLE 15

Lake Huron, District 1. Comparison of the yield in pounds from an average day's fishing with each of six types of fishing gear. The data are based on the assumption that the following lifts represent equivalent amounts of labor on the part of the fishermen; gill nets, 30,000 feet; deep trap nets, 7; shallow trap nets, 11; pound nets, 10; hooks, 2,400

Year	2¾" Gill Net	4½" Gill Net	Deep Trap Net	Shallow Trap Net	Pound Net	Hooks
1929	618	621		574	1,033	775
1930	891	711	1,128	826	1,509	491
1931	942	567	1,037	1,004	1,116	635
1932	861	531	681	937	1,024	606

TABLE 16

Lake Huron, District 1. Summary of Trout Fishery, 1931

Type of Gear	2¾" Gill Net	4½" Gill Net	Trap	Pound	Hook	No Gear Recorded
Catch in gear.....	7,066	286,594	60,236	69,871	112,644	5,750
Percentage of total trout in gear.....	1.30	52.86	11.11	12.89	20.78	1.06
Percentage of gear's catch.....	1.52	57.30	6.84	15.69	99.75	
Percentage of gear with trout.....	78.90	97.85	35.08	79.80	100.00	
Catch per night (effective).....	0.10	3.36	5.77	8.62	66.22	
Catch per night (total).....	0.08	3.30	1.56	6.70	66.22	
Catch per lift (effective).....	0.60	11.09	22.41	21.94	263.80	
Catch per lift (total).....	0.48	10.85	7.86	17.51	263.80	

TABLE 17

Lake Huron, District 1. Data to show the position of the deep trap net in the fishery, 1929-1932

	1929	1930	1931	1932
Total yield of whitefish.....	385,280	692,735	941,768	593,999
Whitefish taken in trap nets.....	1,332	203,903	367,001	160,962
Per cent of total whitefish taken in trap nets.....	0.95	29.43	38.97	27.10
Change in yield of whitefish.....		+307,455	+249,033	-347,769
Change in yield of whitefish from trap nets.....		+202,591	+163,098	-206,039
Change in trap net yield as percentage of total change in yield.....		65.89	65.49	59.25
Catch of whitefish per net lift.....	10.83	135.48	129.55	81.75
Catch of whitefish per net night.....	0.95	40.83	32.72	21.50
Number of net lifts with whitefish.....	123 ¹	1,505	2,833	1,969

¹These lifts probably represent incidental captures of whitefish in shallow trap nets.

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No. 2

Causes of Variation in the Growth Rates of Fishes

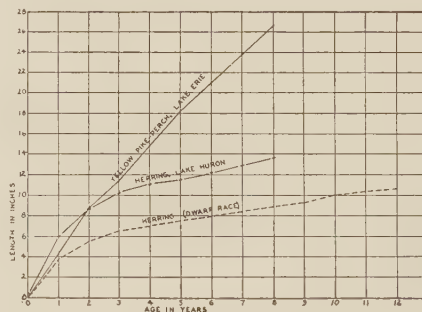
By RALPH HILE

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If a fisherman were asked, "How fast does a fish grow?" he would at once counter with the question, "What kind of fish?" The question would be well taken, for different kinds of fish vary greatly in their capacity for growth. It would be surprising indeed to find a bloater growing as rapidly as a whitefish, or a perch growing after the manner of a yellow pike. Not only do different kinds of fish vary as to their rate of growth; they vary also as to the type of growth. It is possible, for example, to describe a coregonid or herring type of growth in which the growth is rapid for about two years and then quite slow in later life, or a pike-perch type in which the early growth is not exceptionally rapid, but a fairly good growth rate is maintained up to the completion of the seventh or eighth year. All the fish within a population tend to follow closely the typical average growth. A fish which has enjoyed exceptionally good growth in one year ordinarily will show poorer than average growth the next, while on the other hand a fish which has grown poorly during one certain year will probably enjoy better than average growth the next. Thus unusually poor or unusually good growth in early life will be "compensated" in later years.

It should be mentioned incidentally that great size in a fish is not necessarily an absolute indication of rapid

growth. The lake sturgeon for example attains a great size, but when we consider that individuals of this species may attain the venerable age of eighty or a hundred years it can



The above graph shows the total length in inches at different ages for the yellow pike of Lake Erie, for the herring of Lake Huron, and for a dwarf race of herring from an inland lake of northern Wisconsin. Note that the herring growth curves resemble each other in form although the crowded inland lake population grows so slowly that it requires ten years to reach the size attained by the Lake Huron herring in three years. The data for the above curves were obtained from the researches of three bureau of fisheries investigators.

be seen that the size of large sturgeons is the result of continued rather than rapid growth. Still other fish which do not reach a great size may fail to do so only because their average life span is fairly short.

The statement made previously that it is often possible to describe the "type of growth" of a species should not be taken to mean that all popula-

tions of that species grow at the same rate. For example, a fish which grows exactly four inches during each of its first four years of life has the same type of growth as a fish which grows twice as rapidly, or eight inches during each of its first four years of life. As a matter of fact different populations of the same species of fish do vary tremendously as to their rates of growth. These differences in growth rate in different populations of a single species depend largely upon the conditions of the surroundings in which the various populations live. In the following discussion some of the more important of the factors which affect growth rate will be considered.

Water temperature is an important factor in determining the growth rate of fishes. The fish is a cold blooded animal (that is, its body temperature corresponds with that of the surrounding water) and, as is the case in all cold blooded animals, the rate at which its life processes proceed varies directly with variations in temperature. It is well known that during the cold winter months the fish is more sluggish and takes less food than in summer. During this winter period of reduced activity little or no growth occurs. During the warm summer months the higher temperature causes digestion to be more rapid, the fish eats heartily and growth occurs. The amount of growth depends upon the length of the summer and the temperature reached by the water. It is a common observation that fish grow more rapidly in southern lati-

tudes than do their brothers of more northerly regions. The large mouthed black bass will serve as an example. In the warm waters of the Gulf States it is not at all uncommon for bass to reach the length of ten or eleven inches during the first summer of their existence. Contrast this situation with that in Indiana where the bass reaches the legal size of eleven inches in the fourth year of life and with that in Wisconsin where very few bass reach the legal size of ten inches before the fifth year, and many are still undersized in the sixth year. The slower growth of the northern fish is not, however, without its compensations, for fish tend to live longer in northern than in southern latitudes.

Of further interest is the fact that in several species of fish it has been demonstrated that more growth occurs in warm summers than in cold summers. In some instances the growth during an unusually warm summer may be several times as great as during a cold one. This effect of yearly variations in average summer temperature is most noticeable in shallow bodies of water in northerly latitudes.

A second factor of primary importance in determining the rate of growth in fishes is the abundance of food. A fish must have food for two purposes. First there is the problem of "maintenance" food—food which supplies energy for the fish's movements and in adult forms material for the production of spawn. After these basic needs are satisfied the excess food

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Causes of Variation in Fish Sizes

Continued from page 4

can be utilized for purposes of growth. As will be seen the question of the relationship between food and growth is quite complicated.

The actual abundance of the different kinds of food must be considered. An area which is rich in food for one kind of fish may offer but a meagre diet for another. For example suckers thrive best in an area where there is plentiful supply of bottom animals while a chub needs for its subsistence a large supply of plankton organisms. Large, carnivorous fish such as the trout would go hungry in the midst of a plentitude of both bottom and plankton foods. For them a supply of forage fish is necessary. It should be remembered, too, that the diets of fish change as the fish increases in age and size, or may even vary from one season of the year to another.

Of more importance in determining growth rate than the total amount of food present in an area is the actual amount of food available to each individual fish. This quantity depends both on the amount of food present and on the number of fish competing for it. Competition occurs among

fishes of the same species and among fishes of different species but with similar food habits. For example the sucker, sturgeon, and whitefish all feed off the bottom and thus compete with each other for food, but none of these fish competes with the trout whose most important food is the chub. The trout however finds competition in the lawyer.

In some cases the competition for food may be so keen as to result in the dwarfing of the competing individuals. Anyone who has had experience fishing in some small lake filled with undersized half-starved perch will realize how seriously the lack of food may impede growth. Dwarf populations of black bass, rock bass, sunfish, lake herrings, and yet other fish have been observed in the inland lakes of the Great Lakes region.

The years following the World War saw an interesting demonstration of how a change in the number of feeding individuals may affect the average growth rate of a fish population. Particular reference is made here to the plaice—one of the most important fishes of the North Sea area. During the two decades before the war there existed an intensive fishery for the plaice. During the war there was

relatively little fishing; and the number of fish in the plaice stock increased tremendously. At the same time the average growth rate decreased noticeably. With the resumption of intensive fishing after the war the number of plaice on the fishing grounds was again reduced, and the rate of growth increased accordingly. There are many other interesting examples of the relationship between growth rate and the density of fish populations, but the lack of space makes it impossible to present them at this time.

While water temperature and the amount of food available to each individual fish are the most important of the factors which determine the rate of growth in fishes they are not the only ones. Growth may be hindered by any condition adverse to the welfare of the fish as, for example, pollution of the waters, infestation by

parasites, or the presence of bacterial diseases. It is probable that in some cases the addition of small amounts of sewage may increase the fertility of the water, provide more fish food, and thus promote better growth.

In conclusion it might be well to mention the recent observations of a German investigator who proved experimentally that crowding young trout together in a small space reduces the amount they grow regardless of how well they are fed and how clean and wholesome the water in which they live is kept. This factor he called the "space factor" (Raumfaktor) and considered it very important in the explanation of the undersized condition of the individuals of a crowded population.

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GROWTH OF THE WHITEFISH, *COREGONUS CLUPEA-
FORMIS* (MITCHILL), IN TROUT LAKE, NORTH-
EASTERN HIGHLANDS, WISCONSIN

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This study of the growth of the whitefish is based on a small number of specimens taken incidentally in the collection of materials for the investigation of the life history of the lake herring or cisco (*Leucichthys artedi*) in Trout Lake, Wisconsin. Although the available data offer no basis for any detailed analysis of the growth of the whitefish in Trout Lake, they give a satisfactorily reliable general growth curve for this exceptionally slow growing population.

Trout Lake, the location of the limnological laboratories of the Wisconsin Geological and Natural History Survey, is situated in Vilas County in the heart of the lake district of northeastern Wisconsin. According to Juday and Birge (1930) Trout Lake has an area of 1,683 hectares (4,160 acres), a depth of 35.0 meters (115 feet), and lies at an elevation of 493 meters (1,618 feet) above sea level. It is the deepest and next to the largest of the lakes of the northeastern highlands region. Data (made available through the courtesy of Dr. Chancey Juday of the Wisconsin Geological and Natural History Survey) concerning the south basin, in which all whitefish samples were taken, are: total volume, 149,020 thousand cubic meters; Secchi disc transparency, 4.5 meters; color, 3 (platinum cobalt scale); pH, 7.6; conductivity in reciprocal megohms, 77; bound CO₂ in milligrams per litre, 18.7; organic matter of plankton in milligrams per litre 0.92. The data concerning the physical-chemical nature of the water, and the abundance of organic matter of plankton, represent average surface conditions.

In middle and late summer, the time of year in which the samples were collected, the whitefish of Trout Lake lives in the hypolimnion where it finds not only water of suitable temperature but also an abundance of dissolved oxygen (Juday and Birge, 1932). In the same strata inhabited by the whitefish are to be found a very dense population of the cisco (*Leucichthys artedi*), considerable numbers of lake trout (*Cristivomer namaycush*) and a few burbot (*Lota maculosa*). There is probably considerable competition for food between the whitefish and the cisco.

The whitefish collections consist of seventeen fish taken in 1927, two

in 1928, nineteen in 1931 and thirty in 1932. All specimens were taken in gill nets. There are no individual net records for 1927 and 1928, but in 1931 and 1932 whitefish were taken in the following sizes of mesh (stretched measure, in inches): $1\frac{1}{4}$, $1\frac{1}{2}$, $1\frac{3}{4}$, 2, $2\frac{1}{4}$, $2\frac{1}{2}$, and 3. Scale samples, taken from the left side of the body from the area between the lateral line and the base of the dorsal fin, were stored in Bureau of Fisheries scale envelopes. In 1931 and 1932 the data recorded on each envelope included date, standard length in millimeters (total length for a few individuals),¹ weight in grams, sex, state of maturity, and size of mesh in which the fish was taken. The 1927 and 1928 data included only the date and the standard length in millimeters.

In the laboratory three scales, selected on the basis of clearness of sculpturing and symmetry of form, from each fish were mounted on a glass microscope slide in a glycerin-gelatin medium made according to the formula given by Van Oosten (1929). The scales were examined by means of the microprojection apparatus described by Van Oosten (1923). The magnification used was X40.5.

Ages were determined by counting the number of annuli (year-marks) or lines of discontinuity between the growth areas of successive years of life. One of the three scales on each slide was measured. For this purpose a tested millimeter ruler was placed upon the projected image along the antero-posterior axis and the diameters of the successive growth areas determined to the nearest millimeter. The calculation of the growth history of the individual fish was based on the assumption that the ratio of scale diameter to body length is constant at all lengths beyond that at which the first annulus is laid down. Van Oosten (1923) demonstrated that this assumption gives highly reliable results in the calculation of the growth of the whitefish. In the same paper on the basis of the examination of the scales of whitefish of known age, Van Oosten proved that in this species the annulus can be taken as a true year mark.

In spite of the slow growth of the Trout Lake whitefish and the advanced age of the specimens in the collection, little difficulty was encountered in the interpretation of the scale structures. Of the 68 fish studied only one was discarded as having scales wholly unsuited for the determination of age. The age determinations of three other fish were indicated as possibly a single year in error.

Table 1 shows the results of the age determinations and growth calculations. In the preparation of the table corresponding age groups of the different years' collections were combined. The ages designate the number of annuli present, or the number of completed years of life. Although the whitefish spawns in late autumn it is considered that the life of the individual begins at the time of hatching the following spring. Thus a fish in its first summer has no annulus and is a member of the O-group; in its second summer it has one annulus and is a member of the I-group, etc.

¹The ratio, total length in standard length is 0.835 for the Trout Lake whitefish.

TABLE 1. AVERAGE LENGTH IN MILLIMETERS AT TIME OF CAPTURE AND CALCULATED LENGTH AT THE END OF EACH YEAR OF LIFE OF EACH AGE GROUP OF THE TROUT LAKE WHITEFISH (CORRESPONDING AGES OF ALL COLLECTIONS COMBINED). BELOW, GRAND AVERAGE OF THE CALCULATED LENGTHS AT THE END OF EACH YEAR OF LIFE AND ANNUAL CALCULATED GROWTH INCREMENTS. AGE GROUPS MARKED WITH ASTERISKS WERE NOT EMPLOYED IN THE CALCULATION OF THE GRAND AVERAGE.

Age	Number of specimens	Length in millimeters	Calculated length in millimeters at the end of each year of life													
			1	2	3	4	5	6	7	8	9	10	11	12	13	14
XIV	2	374	70	113	144	182	210	232	256	278	297	318	330	342	357	366
XI	1	348	94	118	165	193	220	255	268	288	307	322	338	—	—	—
IX	3	314	71	104	142	173	198	229	253	280	306	—	—	—	—	—
VIII	4	277	80	113	135	162	193	211	241	267	—	—	—	—	—	—
VII	7	264	82	114	150	181	209	232	251	—	—	—	—	—	—	—
VI	17	246	82	120	153	182	209	232	—	—	—	—	—	—	—	—
V	9	224	80	116	150	183	208	—	—	—	—	—	—	—	—	—
IV	12	204	83	120	155	185	—	—	—	—	—	—	—	—	—	—
*III	6	180	95	130	166	—	—	—	—	—	—	—	—	—	—	—
*II	3	195	96	156	—	—	—	—	—	—	—	—	—	—	—	—
*I	3	130	93	—	—	—	—	—	—	—	—	—	—	—	—	—
	67	Grand average	81	117	151	181	207	230	251	275	303	319	333	342	357	366
	Δ	ΔL	81	36	34	30	26	23	21	24	28	16	14	9	15	9

The data of Table 1 show a very close agreement among the calculated growths of the best represented age groups (IV to VII, inclusive). The older, poorly represented age groups show certain irregularities but in general agree well with age-groups IV to VII. The calculated growths for the three youngest age groups, particularly I and II, tend definitely to be higher than those based on fish of greater age. These high calculated growths of the younger age groups are probably the result of selection by the gear used in collecting the samples. Such a conclusion is supported by the observation that the first three age-groups are poorly represented in the samples, whereas they would be expected to outnumber fish of greater age.

At the bottom of Table 1 may be found the data for the general growth of the Trout Lake whitefish, based on a combination of all specimens older than the III-group. (See also Figure 1). The data given include the average calculated length at the end of each year of life and the calculated increment of growth during each year of life. The data show that the first year's growth is more than twice as great as that in any other year of life. The annual increments of growth decrease continuously during the first seven years. The small number

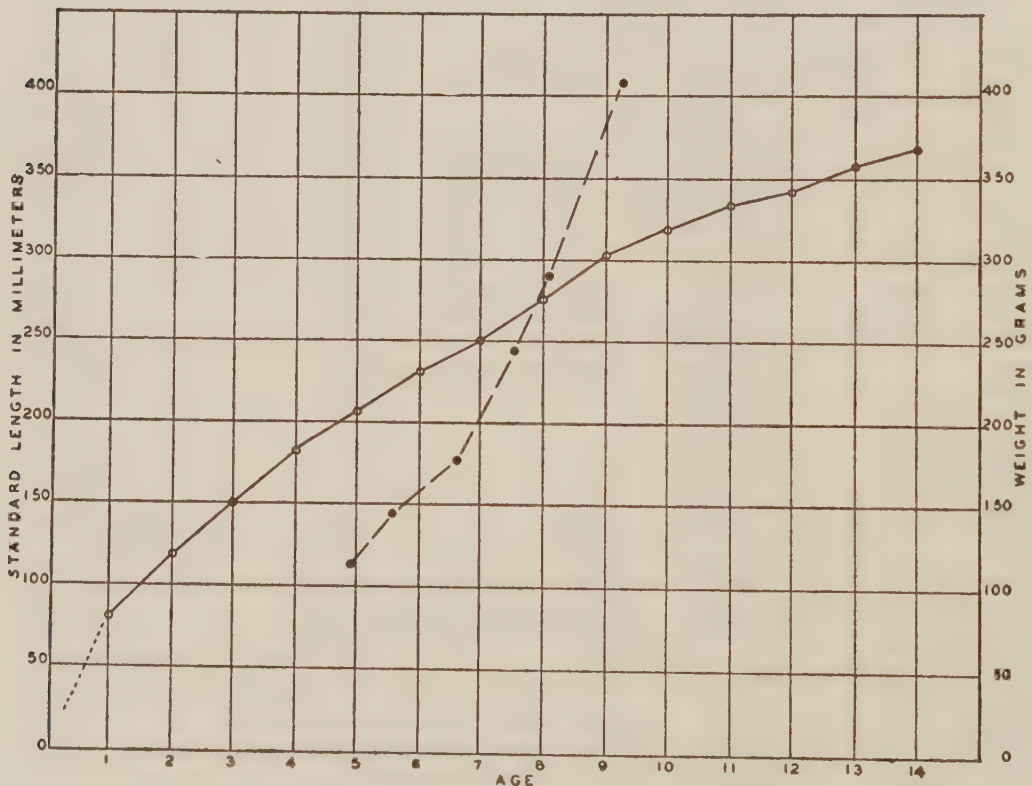


FIGURE 1.—Average calculated length (in millimeters) of the Trout Lake whitefish at the end of each year of life o—o—o, and average weight (in grams) of the various age groups o--o--o.

of specimens in the age groups above the VII-group causes the later portion of the curve for growth in length to be irregular.

Data on the growth in weight of the Trout Lake whitefish appear in Table 2. (See also Figure 1). Here again, the data for the first three age groups must be considered unreliable because of selection by gear. The data of Table 2 do not include the 1927 and 1928 collections for which no weights are available. Along with the weight data are presented the values of the coefficient of condition, the quantity, K , in the equation $W = K \times 10^{-5} L^3$, where W = weight in grams and L = (standard) length in millimeters. It may be seen that although the greatest amount of growth in length occurs in the first year of life, the largest annual increments of growth in weight are found in the later years of life. The values of K show that while the older fish may have a slightly heavier build than the very young ones, there is on the whole little change in the relative heaviness of form with continued growth.

TABLE 2. LENGTH (IN MILLIMETERS), WEIGHT (IN GRAMS), AND CONDITION (K) OF THE DIFFERENT AGE-GROUPS OF THE TROUT LAKE WHITEFISH, BASED ON THE COMBINATION OF THE 1931 AND 1932 COLLECTIONS.

Age group	I	II	III	IV	V	VI	VII	VIII	IX
Number of fish	3	1	2	11	8	12	6	4	1
Standard length	130	164	179	204	220	242	263	277	307
Weight (grams)	25	55	81	113	144	177	244	290	408
ΔW	25	30	26	32	31	33	67	46	118
K	1.14	1.25	1.39	1.31	1.35	1.25	1.34	1.36	1.41

The relative abundance of the sexes in the samples was in the ratio of 162 females per 100 males. The data were inadequate for any study of the relationship between the sex ratio and age. It is probable that none of the fish reach sexual maturity before the end of the fifth or sixth year of life.

The slow growth of the Trout Lake whitefish is brought out sharply by a comparison with the growth of whitefish populations in other localities. Table 3 compares the growth in length of the Trout Lake whitefish with that of the whitefish in Lakes Winnipeg and Winnipegosis (Bajkov, 1930); Shakespeare Island Lake, Lake Nipigon, and Lake Ontario (Hart, 1931); and Hudson Bay (Dymond, 1933). Table 4 shows a comparison of growth in weight for the same populations, with the exception of Hudson Bay. The methods of the various authors of expressing age and weight have been modified, where necessary, to conform with the method used in this study. In order to make the Trout Lake data on growth in length more comparable with those of other workers the average lengths of the different age groups at the time of capture have been used rather than calculated lengths at the end of completed years of life. It may be seen at once that the Trout Lake whitefish has the slowest growth of any of the seven populations. The slow growth in the Trout Lake stock is particularly striking with respect to growth in weight. This slow growth in weight

may depend in part on slenderness of form as well as on the slowness of the growth in length.

TABLE 3. COMPARISON OF THE AVERAGE LENGTHS (IN MILLIMETERS) OF THE DIFFERENT AGE GROUPS OF THE TROUT LAKE WHITEFISH WITH THE AVERAGE LENGTHS OF FISH OF CORRESPONDING AGE IN OTHER WHITEFISH POPULATIONS

Lake	Age										
	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV
Trout	204	224	246	264	277	314	—	348	—	—	374
Hudson Bay	241	260	273	318	358	367	—	—	—	—	—
Ontario (Pleasant Point)	336	346	409	459	—	—	—	—	—	—	—
Nipigon	227	238	251	282	322	358	384	393	400	404	435
Shakespeare Island	231	241	259	286	302	316	348	364	370	371	396
Winnipeg	380	420	450	480	500	520	540	560	575	585	590
Winnipegosis	390	420	450	480	500	520	540	560	575	585	592

TABLE 4. COMPARISON OF THE AVERAGE WEIGHTS (IN GRAMS) OF THE DIFFERENT AGE GROUPS OF THE TROUT LAKE WHITEFISH WITH THE AVERAGE WEIGHTS OF FISH OF CORRESPONDING AGE IN OTHER WHITEFISH POPULATIONS

Lake	Age						
	IV	V	VI	VII	VIII	IX	
Trout	113	144	177	244	290	408	
Ontario (Pleasant Point)	540	790	1,130	1,500	—	—	
Nipigon	140	230	280	400	570	850	
Shakespeare Island	190	220	280	400	450	540	
Winnipeg	772	1,044	1,135	1,362	1,498	1,680	
Winnipegosis	817	1,044	1,135	1,362	1,498	1,680	

The great density of the fish population of Trout Lake in the strata inhabited by the whitefish appears to offer the most logical explanation of the slow growth of the whitefish in that body of water. Although whitefish are not particularly abundant in Trout Lake, they occur along with an extremely dense population of small, slow growing lake herring or ciscoes.² Whether the crowding impedes growth through the creation of intense competition for food or through the operation of a "space-factor," whereby crowding hinders growth independently of competition for food, remains to be demonstrated.

SUMMARY

The whitefish of Trout Lake, northeastern Wisconsin, shows the slowest growth yet recorded for any North American population of that species. This slow growth is probably the result of the great density of the fish population, particularly of the lake herring, in the hypolimnion of the lake. The crowding may impede growth through the creation of intense competition for food or through the operation of a "space-factor."

LITERATURE CITED

Bajkov, Alexander

1930. Fishing industry and fisheries investigations in the Prairie Provinces. Trans. Am. Fish. Soc., Vol. 60, pp. 215-237.

²Hile, Ralph, (MS).—Age and growth of the cisco *Leucichthys artedii* (Le Sueur) in the lakes of the Northeastern Highlands, Wisconsin.

Dymond, J. R.

1933. Biological and oceanographic conditions in Hudson Bay. 8. The coregonine fishes of Hudson and James Bays. Contributions to Canadian Biology and Fisheries, N. S., Vol. VIII, No. 1, 12 pp. Toronto.

Hart, John Lawson

1931. The growth of the whitefish *Coregonus clupeaformis* (Mitchill). Contributions to Canadian Biology and Fisheries, N. S., Vol. VI, No. 20, pp. 429-444. Toronto.

Juday, Chancey, and Edward A. Birge

1930. The highland lake district of northeastern Wisconsin and the Trout Lake limnological laboratory. Trans. Wisconsin Acad. of Sci., Arts and Letters, Vol. XXV, pp. 337-352. Madison.
1932. Dissolved oxygen and oxygen consumption in the lake waters of northeastern Wisconsin. Trans. Wisconsin Acad. of Sci., Arts and Letters, Vol. XXVII, pp. 415-486. Madison.

Van Oosten, John

1923. The whitefishes (*Coregonus clupeaformis*). A study of the scales of whitefish of known ages. Zoologica, Scientific Contributions of the New York Zoological Society, Vol. II, No. 17, pp. 380-412. New York.
1929. Life history of the lake herring (*Leucichthys artedi* Le Sueur) of Lake Huron as revealed by its scales, with a critique of the scale method. Bull., U. S. Bur. of Fish., Vol. XLIV, 1928 (1929), Document No. 1053, pp. 265-428. Washington.

From The Fisherman (Grand Haven, Michigan),
vol. 4, no. 12, pp. 1,2, 1935

Daily Reports Reveal New Facts and Figures

**Relationship Between Fishing Time and Size of Lifts is One
of the Interesting Studies Made From Daily
Reports of Fishermen**

By DR. RALPH HILE
Assistant Aquatic Biologist U. S. Bureau of
Fisheries

(Commercial fishermen are urgently requested to examine the following article carefully and submit their personal opinions on the subject discussed. Letters should be addressed to: Great Lakes Laboratory, U. S. Bureau of Fisheries, University Museums Bldg., Ann Arbor, Mich.)

The significance of the above question can best be brought out by the following example. Let us suppose that two pound nets of identical size and structure fish side by side throughout the entire season, but that one is lifted every day and the other every two days. How will the average size of their lifts compare, and which net will show the greatest total catch for the season? Will the lifts of the pound net visited every two days be twice as large as those of the net that is lifted daily, or will they be only 50 per cent or 25 per cent larger—or again will there be little if any difference in the average size of their lifts? Will the pound net that is lifted every other day take as many fish during the entire season as the net that is lifted daily? For the words "pound net" in the preceding sentences substitute in turn each of the other types of stationary fishing gear employed in the Great Lakes fisheries and you have a complete statement of the problem concerning the effect of fishing time on the size of the lift.

The Bureau of Fisheries' statistical studies of the commercial fisheries of the Great Lakes have brought out some very interesting facts concerning the relationship between fishing time and the size of lift in different types of fishing gear. These data, a small part of which will be presented in this article, have been obtained



Dr. Ralph Hile

from the study of actual records of commercial fishing contained in the monthly report sheets turned in by all licensed fishermen in the State of Michigan.

The studies on pound nets in northern Green Bay (including Big and Little Bay de Noc) offer a typical example of the results obtained. In this area pound nets lifted every two days took only 16 per cent more fish per lift than the nets lifted every day, that is, if a pound net one night out takes 100 pounds of fish the same net two nights out may be expected to take 116 pounds of fish. At three nights out this same net would take 138 pounds of fish; at four nights out—141 pounds; and at five nights out—154 pounds. Although these increases are somewhat irregular, they serve to show that an increase in the length of time a pound net is fished is accompanied by a surprisingly small increase in the average size of the lift.

Using the ratio of 100 to 116, 100 to 138, etc., let us now return to the question of the production, during a season, of nets lifted daily and at longer intervals. Assuming that our sea

Daily Reports Reveal New Facts and Figures

Continued from Page One

son is 60 days long and that a pound net lifted every day will have an average lift of 100 pounds, it may seem that the season's production of this net will be 60 times 100 pounds or 6,000 pounds. If this same net were lifted every two days the lifts would average 116 pounds, but there would be only 30 lifts, and the season's production would be only 3,480 pounds. At three nights out there would be 20 lifts of 138 pounds each for a season's production of 2,760 pounds; at four nights out 15 lifts of 141 lbs. each for a season's production of 2,115 pounds; and at five nights out 12 lifts of 154 pounds each for a season's production of 1,848 pounds. Thus it appears that an increase in the fishing time of a pound net brings about a large decrease in its total production. Although the size of the individual lifts may be increased by as much as 54 per cent (at five nights out) the reduction in the number of lifts much more than compensates this increase.

Approaching the problem from the standpoint of the number of pound nets necessary to produce a certain total season's yield, it may be determined that in round numbers a string of ten nets lifted daily will produce as many fish in the course of a season as 17 nets lifted every two days; as 22 nets lifted every three days; as 28 nets lifted every four days; and as 32 nets lifted every five days. Thus it would seem that in fishing pound nets

Approaching the problem from the standpoint of the number of pound nets necessary to produce a certain total season's yield, it may be determined that in round numbers a string of ten nets lifted daily will produce as many fish in the course of a season as 17 nets lifted every two days; as 22 nets lifted every three days; as 28 nets lifted every four days; and as 32 nets lifted every five days. Thus it would seem that in fishing pound nets the most efficient procedure would be to fish a small number of nets lifted frequently rather than a larger number lifted at longer intervals of time.

The results obtained for other impounding nets—deep traps, shallow traps, and fykes—were closely similar to the results for pound nets.

The relationship between fishing time and the size of the lift in chub nets may be illustrated with the results obtained from the study of chub fishing along the eastern shore of Lake Michigan between Cat Head Point and Holland over the four year period, 1930-1933. In this area a gang of chub nets that takes 300 lbs. of fish when lifted after three nights out may be expected to take 342 lbs. at four nights out, 400 pounds at five nights, 419 pounds at six nights, 482 pounds at seven nights, 490 pounds at eight nights, and 534 lbs. at nine nights. Expressing the data in percentages, it may be stated that a doubling of the fishing time (from three to six nights out) brought about only a 40 per cent increase in the catch. In other words, chub nets fished in this area, fished two and one half times as efficiently in the first three days of a six day period as they did in the last three days.

If the lift of the chub nets three nights out is compared with the lift of nets that fished three times as long, it may be seen that the nets fishing nine days took 78 per cent more fish than nets fishing three days. This relationship may be expressed in another way by saying that of every 178 pounds of chubs taken from nets nine nights out, 100 pounds were taken in the first three days and only 78 pounds in the last six days.

From the figures given in the two

preceding paragraphs, it may be determined that in the course of a season, ten boxes of chub nets lifted every three days will take as many fish as 14 boxes lifted every six days, and as 17 boxes lifted every nine days.

In the large mesh gill-net fishery for trout and white fish along the eastern shore of Lake Michigan between Little Point Sable and Holland an increase in the fishing time from three to six nights out brought a 21 per cent increase in the average size of the lift, and an increase from three to nine nights out brought a 39 per cent increase in the size of the lift. Thus it appears that increasing the fishing time increases the size of the lift twice as much in chub nets as in large mesh gill nets.

In the hook fishery for trout along the eastern shore of Lake Michigan between Cat Head Point and Holland a doubling of the fishing time (from two to four nights out) increased the size of the lift 29½ per cent, and a tripling of the time (from two to six nights out) increased the size of the lift 45½ per cent.

The question of the relationship between fishing time and the average size of the lift has an important bearing on statistical studies of the Great Lakes fisheries, now being carried on by the Bureau. For this reason, we are attempting to obtain all possible information on this point and are particularly desirous of learning the opinions of the commercial fishermen, themselves, on the subject. We should appreciate greatly answers to such questions as: In your experience how much does increase in the number of nights out affect the size of the lift? Do the figures given in this article agree with your observations, and if not, how do they differ? How do you explain the fact that nets tend to become the less efficient the longer they are in the water? To what extent do fish that have once entered a pound, trap, or fyke net make their escape?

Letters should be addressed to: U. S. Bureau of Fisheries, University Museums Bldg., Ann Arbor, Michigan.

U. S. DEPARTMENT OF COMMERCE

Daniel C. Roper, Secretary

BUREAU OF FISHERIES

Frank T. Bell, Commissioner

AGE AND GROWTH OF THE CISCO,
LEUCICHTHYS ARTEDI (LE SUEUR), IN THE
LAKES OF THE NORTHEASTERN
HIGHLANDS, WISCONSIN

By RALPH HILE

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AGE AND GROWTH OF THE CISCO, *LEUCICHTHYS ARTEDI* (LE SUEUR), IN THE LAKES OF THE NORTHEASTERN HIGHLANDS, WISCONSIN ¹

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INTRODUCTION

In 1927 the Wisconsin Geological and Natural History Survey and the United States Bureau of Fisheries instituted a cooperative study of the life histories of the fishes that inhabit the lakes of the highland district of northeastern Wisconsin. By the arrangements agreed upon, the survey furnished facilities for the conduct of field operations and staff members of the two organizations cooperated in the collecting and investigation of the research materials. The limnological laboratories of the survey at Trout Lake, Wis., served as headquarters for all field operations.

During the summer and early autumn of 1927 Dr. Stillman Wright of the Bureau, with the aid of an assistant made collections of fishes from several lakes of the region. In 1928, when it was impossible for Dr. Wright to be in direct supervision of the field work, the collections were made by Dr. Joseph Goldsmith and an assistant. A part of the collections for the years 1927 and 1928 served as a basis for a preliminary report on the growth of the rock bass in Trout and Muskellunge Lakes (Wright, 1929). In 1929 Dr. Wright found it necessary to devote his entire time to limnological investigations on Lake Erie and collecting operations were suspended during that year.

The collection of data for the investigation of the life histories of the fishes of the region was resumed in 1930. During this season the field work was carried on by Dr. Edward Schneberger of the survey and Dr. Ralph Hile of the Bureau. (In 1931 the collecting of materials was continued under the supervision of these 2 investigators with the aid of 2 assistants.) In 1932, when it was impossible for Dr. Hile to participate in the field operations, the collections were made by Dr. Schneberger, aided by one assistant.

Although the materials collected have afforded data on a number of species, the investigations have centered upon the life histories of three forms: The yellow perch, *Perca flavescens* Mitchill; the rock bass, *Ambloplites rupestris* Rafinesque; the cisco or lake herring, *Leucichthys artedii* (Le Sueur). Dr. Schneberger has given his attention to the study of the perch and Dr. Hile to the study of the rock bass and the cisco. The small collections of game fishes collected in the various years formed a part of the material used by Juday and Schneberger (1930, 1933) in their studies on the growth of game fishes in Wisconsin.

The ultimate aim of these studies of the fishes of northeastern Wisconsin is a more precise evaluation of the various environmental factors in their relation to the growth and abundance of the different fish forms. Since 1925 the survey has been conducting extensive limnological investigations on the lakes of the region.² The fish collections that were made for the growth studies have served also as material for study by survey staff members of food habits and parasitic infestation in the various species. The general consideration of the relationship between growth and environment awaits the termination of these several lines of investigation. In the present publication references will be made to relationship between growth and certain environmental factors, but no exhaustive discussion of the question will be undertaken.

In the investigation of the ciscoes an attempt was made to select the populations for study from "type" lakes. The selection of the four lakes with which this study is primarily concerned was based principally on the amount of fixed CO₂ present in

² For a history of the survey's operations consult Juday and Birge (1930). Annual summaries of the survey's activities appear in the Bureau's reports on Progress in Biological Inquiries (Rich, 1926; Higgins, 1928a, 1928b, 1930, 1931a, 1931b, 1932, and 1933).

the water. This factor was considered to be a fair index of the general productive capacity of the various waters. Size and form of basin were also taken into account in the selection of the lakes. Trout Lake is the second largest and the deepest lake of the region. In comparison with the surrounding bodies its water is relatively hard. Muskellunge is a lake intermediate as to size and as to the amount of fixed CO₂. Silver Lake is a small lake with intermediate conditions with respect to fixed CO₂. Clear Lake has an area approximately equal to that of Muskellunge Lake. Its water contains an unusually small amount of fixed CO₂.

Table 1 gives for each lake the details of location, area, depth, and also data relative to the physical and chemical nature of the waters. The two lakes, Allequash and Tomahawk, from which small samples of scales were obtained for growth study, are included in the table.

TABLE 1.—Description of the 6 lakes of which cisco populations were studied

[The characteristics, color, pH, conductivity, fixed CO₂, and organic content of plankton refer to average surface conditions. These data were furnished by the Wisconsin Geological and Natural History Survey]

Lake	Location	Length in kilometers	Width in kilometers	Surface area (hectares)	Maximum depth (meters)	Volume in 1,000 cubic meters	Secchi disk transparency (meters)	Color platinum cobalt scale	pH	Conductivity in reciprocal megohms	Bound CO ₂ in milligrams per litre	Organic matter of plankton in milligrams per litre
Clear.....	Town 39N, range VIIIE.....	2.10	1.83	373	26.5	-----	6.3	0	6.6	17	2.2	0.84
Muskellunge.....	Town 41E, range VIIIE.....	3.30	1.18	375	19.3	26,172	4.0	4	7.3	40	10.0	1.16
Silver.....	Town 41N, range VIE.....	1.69	.64	87.3	19.5	9,884	5.5	4	7.5	62	15.0	.85
Trout:												
North basin.....	{ Town 41 and 42N, range VI	3.60	2.10	532	29.0	69,017	5.0	6	7.8	73	18.5	.66
South basin ¹	{ and VIIIE.	4.51	3.86	1,051	35.5	149,020	4.5	3	7.6	77	18.7	.92
Allequash.....	Town 41N, range VIIIE.....	2.41	1.41	142	7.5	-----	1.5	30	7.9	67	16.9	1.48
Tomahawk.....	Town 38 and 39N, range VI and VIIIE.	7.24	3.00	1,476	22.5	-----	4.2	8	7.6	69	16.7	.78

¹All ciscoes collected from Trout Lake were taken in the south basin.

Juday and Birge (1930) published a general description of the northeastern highland lake district. Thwaites (1929) described the glacial geology of a part of Vilas County in which all but two (Clear Lake and Tomahawk Lake) of these lakes are located. Chemical, physical, and biological data concerning the various lakes have appeared from time to time in the publications of the limnological laboratory of the survey.

From time to time in the following discussion different species of fish will be mentioned by their common names. Because of the considerable local variation in the common names of fishes it is thought well to list the scientific names of the various species mentioned, along with their common names:

Bluegill, *Helioperca incisor* (Cuvier and Valenciennes).

Burbot, *Lota maculosa* Le Sueur.

Ciscoes or chubs, *Leucichthys* spp.

Cisco, lake herring, *Leucichthys artedii* (Le Sueur).

Lake trout, *Cristivomer namaycush* (Walbaum).

Largemouth black bass, *Aplites salmoides* (Lacépède).

Perch, yellow perch, *Perca flavescens* Mitchill.

Pike-perch, *Stizostedion vitreum* (Mitchill).

Rock bass, *Ambloplites rupestris* Rafinesque.

Sauger, *Stizostedion canadense* (Smith).

Smallmouth black bass, *Micropterus dolomieu* Lacépède.

Sucker, *Catostomus commersonnii* (Lacépède).

Whitefish, *Coregonus clupeaformis* (Mitchill).

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Harry C. Carver, professor of mathematics and insurance in the University of Michigan, read the section of the manuscript on the relationship between length and weight.

Dr. Peter Okkelberg, secretary of the Graduate School of the University of Michigan, checked the accuracy of my translation of portions of Huitfeldt-Kaas' (1917) publication. The reference to Olofsson's (1932) paper is based on an abstract prepared by R. W. Eschmeyer of the Michigan Institute for Fisheries Research.

The determination of age and the calculation of growth of the 1928 collection of the Trout Lake cisco are entirely the work of Dr. Stillman Wright, formerly of the Bureau of Fisheries.

MATERIALS

The investigation of age and growth has been based upon the determination of ages for 3,882 specimens and the calculation of growth for 3,694 specimens. Specimens other than those whose ages were determined have been used incidentally for other purposes such as the study of vertical distribution of the cisco and the density of population. Koelz (1931) described material from each of the six lakes whose populations are considered in this study. According to Koelz 3 subspecies of *Leucichthys artedi* are represented in these 6 populations. Clear Lake is the type locality for *L. artedi clarensis* Koelz. The same form is accredited to Muskellunge, Silver, and Allequash Lakes. Koelz described the Trout Lake cisco as *L. artedi clemensi* Koelz, and the form occurring in Tomahawk Lake as *L. artedi wagneri* Koelz. However, Hile (MS.) in a paper now in press has demonstrated that the ciscoes of these lakes at present are not susceptible of division into subspecies, but should be considered merely as populations of the species, *L. artedi*.

Table 2 lists the locality and year of capture of the ciscoes used in the life-history studies. The 1931 material includes 658 preserved specimens collected for a morphometric study to appear in a later publication, while all the 1932 Muskellunge Lake specimens and 95 of the 1932 Clear Lake specimens were preserved.

TABLE 2.—Year of collection and number of specimens in the collections used in the study of age and growth of the cisco

Lake	Year of collection				Total number
	1928	1930	1931	1932	
Trout.....	182	508	610	—	1,300
Muskellunge.....	281	245	616	188	1,330
Silver.....	135	118	378	—	631
Clear.....	—	—	249	191	440
Allequash.....	47	66	—	—	113
Tomahawk.....	68	—	—	—	68
Total.....	713	937	1,853	379	3,882

The relatively limited data from the small collections from Allequash and Tomahawk Lakes are not considered in the general discussions of this paper, but are treated in a special section (appendix A).

METHODS

GEAR USED IN COLLECTING

With the exception of a small number of 0-group individuals picked up on the beaches of Trout Lake all samples used in this investigation were collected by means of gill nets. The 1928 collections were made in nets of the following sizes of mesh: ³ 1¾, 1½, 1¼, 2, 2½, and 3 inches, and in Trout Lake a 1¼ by 8-inch trammel. The trammel used in the capture of Trout Lake ciscoes would operate as a 1¼-inch gill net. In this year no net records were kept for individual specimens. It is unlikely, however, that in any of the three populations (Trout Lake, Muskellunge Lake, Silver Lake) ciscoes were taken either in the 2½-inch- or 3-inch-mesh nets.

The nets used in 1930 had also been used in 1928. However, the discarding of worn-out nets at the close of the 1928 season was so extensive that the only sizes of mesh available in 1930 for the capture of ciscoes in the three lakes named in the preceding paragraph were 1½ and 2 inches. These same nets were used in the early part of the 1931 collecting season. The depth of these nets varied from 3 to 4½ feet.

The gill nets used in 1930 and in the early part of the 1931 season were in a sorry state of repair. Not only were many of the meshes broken, but holes of considerable size were of frequent occurrence. The making of repairs was not feasible as the thread had deteriorated to the extent that even ordinary handling and use of the nets frequently produced new tears in the webbing.

The gear was completely replaced on July 22, 1931, after which date the following sizes of mesh were used: 1¼, 1½, 1¾, 2, 2¼, 2½, and 3 inches. Each net was 50 yards long and approximately 6 feet deep; 5-inch leads were used as a precaution against tangling of leads in the webbing. All Clear Lake samples (1931 and 1932) were taken in the new gear, but only a few lifts of the new gear were made in the other lakes.

The question of gill net selectivity, particularly with reference to the use of gill net samples for the study of age and growth, is considered in a special section (pp. 294–306).

METHODS OF FISHING

The new nets purchased in 1931 were fished in gangs containing 1 net of each of the 7 mesh sizes. In sets of the old nets the larger mesh sizes, known to be ineffective on the cisco populations that were being sampled, were occasionally

³ Throughout this paper, sizes of mesh, unless otherwise indicated, are presented as stretched measure.

omitted. No attempt was made to arrange the nets in any definite order as to size of mesh. In general it was customary to intersperse the larger mesh sizes with the smaller. All sets were made on the bottom.

The nets were lifted and reset once each day. At least once each week they were removed from the water, stretched on a reel, and allowed to dry thoroughly. At intervals of about a month all the nets were treated with copper soap after a method suggested by Harry Hansen, formerly of the Bureau of Fisheries.

The 1928 data contain only scattered information as to the depth from which the various samples were taken. During 1930 observations were made regularly as to the general depth and the nature of the bottom in the region in which the nets were set. Later it was found desirable to possess more precise information on the matter of depth. Accordingly in 1931 and 1932 soundings were made to determine the depth at which each particular net was set. Routine records were kept as to the condition of the weather (cloudiness, precipitation, and strength and direction of the wind). Catches from the different sizes of mesh were placed separately in labeled pails. After the return to the field laboratory counts of the number of fish taken in each net were added to the field notes.

FIELD DATA RECORDED FOR INDIVIDUAL SPECIMENS

Scale samples were taken in the field from all specimens except those preserved for morphometric studies. (The treatment of preserved specimens will be discussed later.) The scale samples were removed whenever possible from the left side of the body dorsal to the lateral line and ventral to the dorsal fin. Scales were stored in standard Bureau of Fisheries scale envelopes. On each serially numbered envelope were recorded date, locality, species, length, weight, sex, state of maturity,⁴ and gear.⁵ The field numbers included in the day's catch were cataloged.

The standard length (from the tip of the snout to the end of the vertebral column) was measured for each individual fish. Enough measurements of the total length (from the tip of the snout to the line connecting the tips of the extended caudal fin) were made to obtain a reliable figure for the ratio between standard and total length.⁶ All lengths were measured with a steel tape in a straight line between the points indicated, not along the curvature of the body, and were recorded to the nearest millimeter. Throughout this paper the unit of length can be assumed to be the millimeter.

The smaller individuals were weighed on a Chatillon spring platform balance of 500-gram capacity with calibrations at 2-gram intervals. Weights of these fish were estimated to the nearest gram. Weight records above 500 grams were obtained by means of a Chatillon spring platform balance of 5-kilo capacity and with calibrations at 20-gram intervals. Weights of these larger fish were estimated to the nearest 5 grams. Toward the close of the 1931 collecting season the smaller balance developed a fluctuating error that was at no point greater than 2 grams. This balance was replaced by a new instrument at the beginning of the 1932 season.

⁴ A fish whose sexual condition showed that it would spawn in the coming autumn was listed as mature, whether or not it may have spawned previously.

⁵ Sex, maturity, and gear were not recorded for the 1928 samples.

⁶ The ratio, total length in standard length, has the following values: Clear Lake, 0.84; Trout Lake, 0.84; Silver Lake, 0.85; Muskellunge Lake, 0.85; Allequash Lake, 0.84. The ratio was not determined for the Tomahawk Lake cisco.

TREATMENT OF PRESERVED SPECIMENS AND RESULTING SHRINKAGE

Part of the fish preserved for morphometric study were weighed and measured while fresh. These specimens were provided with individual, serially numbered tin tags. Other specimens to be preserved were divided into small groups which were wrapped in cheesecloth. Within each package was included a label bearing a record of date, locality, and usually of gear. The specimens were held in a 10-percent formalin solution until the close of the season. Upon removal from the formalin solution the fish were soaked in water about 4 days and then transferred permanently to a 70-percent solution of alcohol.

Since the preserved specimens—most of which were not weighed and measured in the field—constituted a part of the material used for a study of growth, it was of some importance to know the extent of the shrinkage brought about by the preserving fluids. Data on this question were obtained from 99 ciscoes from Clear Lake and from 105 ciscoes from Muskellunge Lake, all taken in 1932. These fish were weighed and their lengths measured at the time of capture. The dates of capture for the Clear Lake specimens were July 12 to July 19; for those from Muskellunge Lake, July 28 and July 29. The individuals of both collections were reweighed and remeasured October 10 and October 11, 1932. At this time they had been in alcohol about 5 weeks. The measurements and weighing of both the fresh and preserved material were made by the same method and by the same individual (Dr. Schneberger).

The ratio between preserved length and fresh length was 1.000:1.019 for the Muskellunge Lake cisco. This value of the shrinkage factor agrees closely with the figure, 1.016, determined by Van Oosten (1929) for the Lake Huron herring. Since the populations from Silver Lake and Trout Lake do not have greatly dissimilar length ranges (approximately 125–200 millimeters) the shrinkage factor based on the Muskellunge ciscoes has been used in correcting for shrinkage the lengths of the preserved specimens from these two lakes.

In the Clear Lake cisco, where the length range is much greater, the relative amount of shrinkage was found to vary at different lengths. The lengths of preserved specimens from this lake were corrected according to the following shrinkage factors:

Length interval:	Shrinkage factor	Number of specimens
350-----	1.005	16
250-349-----	1.010	65
150-249-----	1.028	18

The shrinkage factors for weight were 1.181 for the Muskellunge Lake ciscoes and 1.144 for the Clear Lake ciscoes. However, the individual shrinkage in weight varied so widely that it was not considered valid to employ a weight shrinkage factor for the purpose of making individual corrections. Only those preserved specimens that were weighed when fresh were used for the study of growth in weight.

PREPARATION AND EXAMINATION OF SCALE MATERIAL

Scales were soaked in water and cleaned by means of a dissecting needle and a small camel's-hair brush. Three scales from each fish were mounted on a microscope slide in a gelatin-glycerin medium prepared according to a formula presented by Van Oosten (1929). No regenerated scales or scales with abnormal or irregular shape

were mounted. On the label of each slide were recorded the field number, laboratory number, date and locality of collection, species, sex, maturity, length, weight, and gear. The scales were studied by means of the projection apparatus described by Van Oosten (1923). The magnifications used were X19 for scales of the Clear Lake ciscoes and X40.5 for scales of all other fish.

MISCELLANEOUS CONSIDERATIONS

It is the policy throughout this paper to apply toward the solution of each particular question all suitable data available. As a result of this procedure there appear certain discrepancies in the number of specimens listed in the tables pertaining to different phases of the general problem of the life history of the cisco. Since discrepancies of this sort, if unexplained, may prove a considerable annoyance to a reader, attention will be called to the causes for at least the most important of them.

Table 2 lists the fish upon which determinations of age were made. These specimens, with the exception of the 1932 Muskellunge Lake collections, separated into age groups and year classes, appear in the growth tables 3 to 7. The tables of general growth in length (10 to 14) are based on fewer specimens than tables 3 to 7 since certain indicated age groups were eliminated because of selection by gear. (The 17 0-group Trout Lake ciscoes were also omitted in the computation of the general growth curve.) The tables for growth in weight (15 to 18) are based on fewer specimens than those for growth in length since part of the preserved fish used in the growth study were not weighed before preservation. Of course, the study of the length-weight relationship and of condition was based only on specimens weighed in the field.

In the listing of catch per unit effort of gill nets (section on the relationship between density of population and rate of growth) it was, of course, valid to include fish that had not been aged. Similarly in the determination of the average length of all fish taken in a particular size of gill net (section on selective action of gill nets) it was also valid to include unaged fish. Further, the grand average length used for comparing the average length of an age group as determined from the combined catch of several different sizes of mesh with the average lengths of the same age group as based on the catch of individual sizes of mesh may include certain fish for which net records were not available. (Net records were lacking for a large part of the preserved fish.) The data of tables 40 and 73 are based in part on catches of Muskellunge Lake ciscoes taken in 1932 for morphometric investigations and included only incidentally in this study. None of the 1928 data is included in the analysis of net catches.

The 1928 data also lacked records of sex and maturity and hence could not be included in the sections on sex ratio and age at maturity.

Although some of these discrepancies are mentioned in the general discussions, a general statement of their origins was considered advisable.

THE SCALE METHOD

ASSESSMENT OF AGE AND CALCULATION OF GROWTH

The treatment here of the growth data of the cisco is based upon the use of the scale method. Van Oosten (1929) established the validity of the method for this species in his study of the life history of the Lake Huron herring. It is assumed that

the method is equally valid for the populations considered in this investigation. As will appear later, the results of the analysis of the growth material presented here seem to justify the assumption. Throughout this paper the individual ages are designated as the number of years of life that have been completed. Although the cisco spawns in late autumn or early winter, the life of the individual is assumed to begin the following spring when hatching takes place. During the first year of its life the individual is a member of the 0 group, during the second year it is a member of the I group, etc. Fish hatched in the same year belong to the same year class, regardless of their age at the time of capture.

Two examinations for age determination were made of the scales of each individual specimen. At the second examination either a definite assignment of age was made for the troublesome scales or the slides were marked as unreadable. At the time of the final examination one of the three scales on the slide was measured. This scale was selected on the basis of clearness of markings and symmetry of form. The diameters of the different growth areas were measured along the anteroposterior axis of the scale. For this measurement the ruler was placed in such a position that its edge passed through the focus of the scale and approximately bisected the posterior field (that portion of the scale which is exposed in its natural position on the fish). Scale measurements were made with a tested millimeter ruler and recorded to the nearest millimeter (occasionally the nearest half millimeter).

The assessment of age was based on the determination of the number of annuli or lines of discontinuity between growth areas of succeeding years. Two difficulties were encountered in the determination of individual ages. The later annuli of the older individuals (particularly those of the slower-growing populations) were sometimes so crowded together as to make their recognition difficult or even impossible. In the latter case the scales were discarded. Accessory annuli (summer checks) were not infrequent, but their characteristically indefinite appearance and their position with respect to the true annuli were such that they were ordinarily easily recognizable. Somewhat less than 5 percent of the total number of scales examined were discarded as unsatisfactory for the determination of age.

Accessory checks were found to occur regularly in all the samples of the scales of the Muskellunge Lake cisco. They could be separated from the true annuli quite easily in the growth fields of the earlier years, and consequently they presented no great difficulty in the age and growth analysis of the earlier (1928-31) collections which were composed almost entirely of I-, II-, and III-group fish. In 1932, however, IV-group fish were present in abundance for the first time. In this year's collection the presence of accessory annuli, along with the IV-group's excessively slow growth during the fourth year of life, made the separation of the III group and the IV group of that year's collection both difficult and uncertain. Because of these difficulties and because of the abundance of data from the preceding years, the 1932 collections were not used in the computation of a general growth curve for the Muskellunge Lake population. However, certain of the data from the 1932 Muskellunge Lake samples will be used from time to time for other purposes.

Van Oosten (1929) demonstrated that after the formation of the first annulus the ratio of the total scale length to body length is so nearly constant in the lake herring that the assumption of the absolute constancy of the ratio affords the most

satisfactory means for the calculation of growth during the various years of the individual's existence. The formula used in the calculation of growth was:

$$L_n = D_n \frac{L_T}{D_T}$$

where

L_T =length of fish at time of capture;

D_T =total diameter of scale;

L_n =length of fish at end of n^{th} year of life;

D_n =diameter of scale within the n^{th} annulus.

Tables 3 to 7 present the data for the calculated growth in length for the ciscoes of Trout, Muskellunge, Silver, and Clear Lakes. Since no difference in the growth of the two sexes was apparent in the fish of the first three lakes the data for these lakes as presented represent a combination of males and females. In the data for the Clear Lake cisco the sexes are treated separately.

TABLE 3.—*Calculated growth of Trout Lake ciscoes to the end of each year of life for the different year classes at each age; sexes combined*

[Groups marked with asterisks unreliable because of selective action of gear]

Year class	Year of capture	Age	Number of specimens	Length in millimeters	Year of life											
					1	2	3	4	5	6	7	8	9	10	11	12
1919.....	1931	XII	1	226	80	104	117	130	148	169	180	190	199	211	218	224
1920.....	1931	XI	2	205	75	103	119	130	142	152	162	172	180	198	204	---
1922.....	1931	IX	2	200	83	112	127	140	154	168	180	190	198	---	---	---
1923.....	1931	VIII	5	192	87	115	134	145	156	169	179	190	---	---	---	---
1924.....	1928	IV	17	147	85	120	133	143	---	---	---	---	---	---	---	---
	1931	VII	4	175	80	113	128	141	153	162	174	---	---	---	---	---
1925.....	1928	III	61	143	84	123	137	---	---	---	---	---	---	---	---	---
	1930	V	9	167	82	116	135	148	160	---	---	---	---	---	---	---
	1931	VI	12	165	79	116	132	145	156	164	---	---	---	---	---	---
1926.....	1928	II	102	134	82	117	---	---	---	---	---	---	---	---	---	---
	1930	IV	99	156	82	118	137	147	---	---	---	---	---	---	---	---
	1931	V	79	156	81	118	135	145	154	---	---	---	---	---	---	---
1927.....	1928	*I	2	128	97	---	---	---	---	---	---	---	---	---	---	---
	1930	III	347	149	79	117	139	---	---	---	---	---	---	---	---	---
	1931	IV	269	148	78	115	135	146	---	---	---	---	---	---	---	---
1928.....	1930	*II	36	140	91	127	---	---	---	---	---	---	---	---	---	---
	1931	III	173	142	84	120	137	---	---	---	---	---	---	---	---	---
1929.....	1931	*II	61	136	87	127	---	---	---	---	---	---	---	---	---	---
	1930	0	17	66	---	---	---	---	---	---	---	---	---	---	---	---
1930.....	1931	*I	2	128	106	---	---	---	---	---	---	---	---	---	---	---

TABLE 4.—*Calculated growth of Muskellunge Lake ciscoes to the end of each year of life for the different year classes at each age; sexes combined*

[Groups marked with asterisks unreliable because of selective action of gear]

Year class	Year of capture	Age	Number of specimens	Length in millimeters	Year of life			
					1	2	3	4
1925.....	1928	III	10	172	105	142	162	---
1926.....	1928	II	252	160	99	147	---	---
1927.....	1928	*I	19	137	97	---	---	---
	1930	III	14	166	85	132	157	---
	1931	IV	2	176	90	143	161	174
1928.....	1930	II	214	162	95	143	---	---
	1931	III	347	166	96	145	163	---
1929.....	1930	*I	17	148	103	---	---	---
	1931	II	258	149	98	138	---	---
1930.....	1931	*I	9	136	96	---	---	---

TABLE 5.—Calculated growth of Silver Lake ciscoes to the end of each year of life for the different year classes at each age; sexes combined

[Groups marked with asterisks unreliable because of selective action of gear]

Year class	Year of capture	Age	Number of spec-imens	Length in milli-meters	Year of life						
					1	2	3	4	5	6	7
1923.....	1928	V	10	182	76	115	142	161	175	-----	-----
1924.....	1928	IV	69	174	79	125	150	166	-----	-----	-----
	1930	VI	3	197	72	112	134	161	177	192	-----
	1931	VII	1	201	77	111	135	158	172	186	196
1925.....	1928	III	46	165	73	127	157	-----	-----	-----	-----
	1930	V	25	193	74	120	145	165	185	-----	-----
	1931	VI	21	194	78	119	142	153	177	189	-----
1926.....	1928	II	9	157	90	140	-----	-----	-----	-----	-----
	1930	IV	58	183	78	126	152	173	-----	-----	-----
	1931	V	108	188	80	126	150	168	182	-----	-----
1927.....	1928	*I	1	133	95	-----	-----	-----	-----	-----	-----
	1930	III	25	181	77	134	167	-----	-----	-----	-----
	1931	IV	102	183	80	132	159	176	-----	-----	-----
1928.....	1930	II	7	173	99	151	-----	-----	-----	-----	-----
	1931	III	61	177	83	137	166	-----	-----	-----	-----
1929.....	1931	II	19	171	104	151	-----	-----	-----	-----	-----
1930.....	1931	*I	66	141	105	-----	-----	-----	-----	-----	-----

TABLE 6.—*Calculated growth of Clear Lake ciscoes (males) to the end of each year of life for the different year classes at each age*

Year class	Year of capture	Age	Number of specimens	Length in millimeters	Year of life								
					1	2	3	4	5	6	7	8	9
1923	1931	VIII	3	338	118	203	248	279	297	314	326	333	
	1932	IX	1	355	114	194	254	290	310	323	333	345	354
1924	1931	VII	8	331	110	198	249	279	298	312	324		
	1932	VIII	7	345	108	195	250	279	302	318	331	342	
1925	1931	VI	11	328	108	192	248	282	303	316			
	1932	VII	9	336	102	188	248	280	302	318	331		
1926	1931	V	4	325	110	189	247	290	312				
	1932	VI	2	320	98	183	251	283		315			
1927	1931	IV	10	317	104	190	258	292					
	1932	V	7	320	98	181	249	288	312				
1928	1931	III	26	285	104	188	255						
	1932	IV	11	314	105	191	260	302					
1929	1931	II	34	253	108	200							
	1932	III	23	290	110	198	268						
1930	1931	I	20	178	119								
	1932	II	20	254	113	218							
1931	1932	I	20	176	122								

TABLE 7.—Calculated growth of Clear Lake ciscoes (females) to the end of each year of life for the different year classes at each age

[illegible]

From an examination of the tables for Trout, Muskellunge, and Clear Lakes it will be noticed that "Lee's phenomenon" of "apparent decrease in the calculated growth" as it is determined from successively older groups of individuals, while possibly present, is not a source of any great discrepancies, especially where large numbers of individuals are involved. On the whole the calculated growths based on different age groups in the same year's collection or upon samples of the same year class taken at different ages, agree satisfactorily for corresponding years of life, with the exception of the large calculated growths obtained for the younger age groups (marked with asterisks in the tables) in the Trout Lake and Muskellunge Lake collections. These large growths can be explained as the result of the selective action of the gill nets used for their capture. (See section on gill net selectivity.) The small but fairly consistent discrepancies that appear in the corresponding calculated growths of older year groups of the Trout Lake fish may be partly the result of slight changes in the body scale ratio. It is probable that selective action of gear plays a role here also. At any rate the discrepancies are of such small magnitude that they affect but little any conclusions that might be drawn concerning the growth of the population as a whole.

LEE'S PHENOMENON IN THE SILVER LAKE CISCO

In the Silver Lake data (table 5) there appear much more pronounced disagreements among the corresponding calculated growths of different age groups than are present in the other three populations. Not only are these discrepancies relatively large, but the comparison of any two age groups shows that in general they tend to be cumulative with increased age. These discrepancies appear in the comparisons of calculated growths based on the same year class but taken in different seasons as well as in calculated growths based on the different age groups of a single year's collection. To illustrate these two points there may be examined (table 5) first the calculated growths of the III, V, and VI groups of the 1925 year class and second the calculated growths of the III, IV, V, and VI groups of the 1931 collection. With certain exceptions in the first year of life it will be noticed that each successively older age group tends to give smaller values for the calculated lengths for corresponding years of life. Thus it may be seen that the observed discrepancies in the calculated growths depend on the differences in the age of the groups studied.

It will be noticed further that the apparent change of growth rate as it appears in the fish older than the II group differs from Lee's phenomenon as it ordinarily occurs, in that it is the calculated growths of the later rather than the earlier years of life that are affected most.

The calculated lengths of the Silver Lake ciscoes at the end of the first year of life require some special consideration. If size of sample is taken into account, the calculated growths for the first year of life show fairly good agreement for all age groups older than II. The calculated growths for the first year of life as based on the II group are somewhat less than those based on the I group, but those of both groups are considerably greater than the growths based on the older-age groups. The high calculated growths for the first year of life as based on the I group can be explained in part by the selective action of the gill nets used in collecting the samples, for there is reason to believe that even the smallest mesh of these nets may have taken only the larger individuals of this group. Such an explanation, however, does not seem to hold for the fish of the II group, since on the basis of comparisons with samples from other lakes the range of size of the Silver Lake II group seems to be such that very little

selection by gear could have taken place. Some other explanation must be sought, therefore, for the high growth values of this age group.

Since disagreements in the calculated growth data of fish are generally attributed in part to changes with age in the growth relation between body and scale, it was deemed advisable to study this relationship in the Silver Lake cisco. The 1931 collection was selected as best suited for this purpose. As was mentioned previously (p. 216) the scale samples used in this entire investigation were all taken from the same region of the body. Selections of scales for mounting and for measuring were made on the basis of distinctness of the annuli and symmetry of form rather than on size. As a consequence of this procedure the relationship between the length of body and the diameters of the scales measured should be comparable in the different age groups of a single sample.

As may be seen in table 8 the average ratio between the body length and the magnified diameters of the scales does not vary greatly from one age group to another. The generally made assumption of a linear relationship between scale size and body size tends to the determination for the Silver Lake cisco of the equation:⁷

$$L=10.7 \text{ mm}+1.078 D,$$

where L =length of body in millimeters,

and D =the (magnified) diameter of the scale in millimeters.

TABLE 8.—*The body-scale ratio for the different age groups of the Silver Lake cisco collected in 1931, and the average diameters of scales as measured at the magnification $\times 40.5$*

[D_T is total diameter. The diameters within the different growth areas of the scales are indicated by the subscript figure]

Age	Number of specimens	Body-scale ratio	D_T	D_1	D_2	D_3	D_4	D_5	D_6	D_7
VII.....	1	1.16	174.0	67.0	96.0	117.0	137.0	149.0	161.0	170.0
VI.....	21	1.16	168.3	67.5	104.0	123.7	139.5	153.6	164.5	
V.....	108	1.13	167.9	70.9	112.6	133.8	150.5	162.6		
IV.....	102	1.13	161.9	71.0	117.5	140.8	155.7			
III.....	61	1.15	155.7	72.6	119.5	145.7				
II.....	19	1.18	145.8	88.0	128.7					
I.....	66	1.17	121.3	90.2						

Table 9 gives a comparison of the calculated growths of the 1931 Silver Lake collection first as they were determined on the assumption of a constant body scale ratio at all ages and second as they appear after correction for the changing body-scale relationship indicated by the above equation. It will be noticed that while the "correction" produced changes in the actual values of the individual average calculated lengths, it did little toward the elimination of the discrepancies between the calculated growths of the different age groups. For example, it may be seen that the maximum discrepancy in the calculated growth for the first year of life (between the calculations for the I group and the VI group) was reduced from 28 millimeters in the uncorrected to 24 millimeters in the corrected data—an improvement in agreement of only 4 millimeters. Similarly, the improvements in the agreement in the calculated lengths for the later years of life are unimportant when they

⁷ It is realized that a more precise evaluation of the body-scale relationship might have been obtained through the use of "key" scales selected from exactly the same location in each fish. However, the complete failure of the "correction" equation to eliminate the discrepancies in the calculated growths of the Silver Lake cisco together with the fact that no corrections are needed in the other three populations made any detailed study of the body-scale relationship in these cisco populations unnecessary.

are considered in relation to the total discrepancy. Thus it may be seen that the observed discrepancies in the calculated growth of the Silver Lake cisco did not originate in a change of the body-scale relationships with increasing age.

TABLE 9.—*Calculated growth of the Silver Lake cisco, collection of 1931*

Age	Length	Uncorrected calculated lengths							Corrected calculated lengths						
		L ₁	L ₂	L ₃	L ₄	L ₅	L ₆	L ₇	L ₁	L ₂	L ₃	L ₄	L ₅	L ₆	L ₇
VII.....	201	77	111	135	158	172	186	196	84	116	138	160	173	187	196
VI.....	194	78	119	142	158	177	189	-----	84	123	145	160	178	189	-----
V.....	188	80	126	150	168	182	-----	-----	86	129	152	169	182	-----	-----
IV.....	183	80	132	159	176	-----	-----	-----	86	135	160	176	-----	-----	-----
III.....	177	83	137	166	-----	-----	-----	-----	89	139	167	-----	-----	-----	-----
II.....	171	104	151	-----	-----	-----	-----	-----	108	152	-----	-----	-----	-----	-----
I.....	141	105	-----	-----	-----	-----	-----	-----	108	-----	-----	-----	-----	-----	-----

Further light is thrown on the question by the examination of the actual average measurements of the growth areas of the scales upon which the Silver Lake growth calculations were based (table 8). The comparison of the diameter measurements of table 8 with the corresponding calculated lengths of table 9 shows clearly that the disagreements in the calculated growths of the different age groups appear also in the actual scale measurements upon which the growth calculations were made. Van Oosten (1929) also observed that Lee's phenomenon was to be found in actual scale measurements as well as in calculated growths.

The "apparent change in growth rate" in the Silver Lake cisco must, then, be considered a real change rather than an apparent change due to changing body-scale relationships. Since, as was pointed out previously, the phenomenon appears consistently both in comparisons between different age groups of the same year class and in comparisons between different age groups of different year classes taken in the same calendar year, it cannot be explained either on the basis of inherent differences in the capacity for growth in different year classes, or on the basis of varying environmental conditions affecting growth in different years. It must rather be considered the result of some selectional factor correlated with the length of time intervening between the years for which the computations and scale measurements were made and the year when the fish was captured. Attention will be called briefly to possible sources of selection.

POSSIBLE CAUSES OF LEE'S PHENOMENON IN THE SILVER LAKE CISCO

SELECTION BY GEAR

A more detailed consideration of the question of the selective action of the gear used will be presented later in this paper. (See section on selective action of gill nets.) It may be stated here, however, that this factor most probably does not operate on the Silver Lake ciscoes except in the I group and that therefore it cannot explain Lee's phenomenon in these fish.

SELECTION DUE TO DISSIMILAR DISTRIBUTION WITHIN THE LAKE OF THE VARIOUS ELEMENTS OF THE POPULATION

Since the gill nets used in collecting the cisco samples for these studies were set directly on the bottom they fished only the lower few feet of water. If it is assumed that the larger individuals of the population tend to lead a more pelagic existence

than the smaller ones, then the more rapidly growing fish within an age group would be less subject to capture by nets set on the bottom than the slower growing individuals within the same group. Further, the effect of such segregation would be greater as age increases. The above-mentioned assumption would serve well to explain decreasing growth as it has been observed in the Silver Lake cisco, but data for its verification are not available. The chief objection to such an explanation lies in the fact that it is the smaller fish not the larger that would normally be expected to lead the more pelagic existence.

SELECTION DUE TO DIFFERENTIAL MORTALITY, CORRELATED WITH GROWTH RATE

It has been observed repeatedly that poikilothermous organisms tend to grow more slowly and reach a greater age in northern latitudes. The phenomenon appears to depend on the relation of temperature to the rate of metabolism. It is not wholly unreasonable to assume that the individual rate of metabolism might affect the individual growth rate and the individual length of life. Were mortality greater among individuals of more rapid growth, those individuals that survived longest would be those that had actually grown most slowly. The early growth as calculated from these slow growing survivors of the older age groups would naturally be small. Further, the effect on calculated lengths of this selection through differential mortality would tend to be increased with greater age, and thus discrepancies of the type observed in the Silver Lake data would be explained.

The relation between individual growth rate and individual length of life has been studied experimentally by several investigators. Osborne et al. (1917) found that a temporary preliminary stunting delayed maturity and extended the life span of rats. Titcomb et al. (1928) and McCay et al. (1931) found that trout that did not grow lived longer than those which showed growth on a similar diet. Zabinski (1929) by effecting a retardation of growth was able to prolong life in the black beetle and the roach. McCay (1933) presented a brief discussion of the general problem of the relationship of rate of growth to longevity.

OTHER POSSIBLE CAUSES

It is recognized that the three possible causes of Lee's phenomenon in the Silver Lake cisco discussed in the preceding paragraphs are by no means the only possible explanations of the observed discrepancies in calculated growth as based on fish of different age. These three suggested explanations were emphasized because they appear to be the most plausible in the face of the available data. Other explanations should be mentioned briefly along with the reason for their rejection.

1. Growth may be better in some calendar years than in others. This explanation cannot be accepted as the growth discrepancies were found to occur between members of the same year class, captured at different ages.

2. Portions of the scale may be resorbed after being laid down. The examination of the scales offered no evidence for any kind of resorption.

3. The scale fields may contract after being laid down. The nature of the structure of scales makes this explanation totally unacceptable. (See Van Oosten, 1929.)

4. More than one annulus per year may be formed. The clarity of scale markings on the Silver Lake cisco was superior to that of the Trout Lake and Muskellunge Lake ciscoes; yet the measurements of the scales of the last two populations gave

quite consistent results in the calculation of growth. Accessory annuli were rare in the Silver Lake cisco scales. With the elimination of the more questionable scales it appears unreasonable to assume that the number of errors in the determination of ages was sufficient to account for the observed large discrepancies in the calculated growths. Certainly accessory annuli cannot account for the decrease with age in the diameter of the first growth field.

5. The individuals of the population may have segregated themselves on the basis of maturity with the result that the smaller, immature members of each age group may have been absent from the samples. This explanation lacks plausibility in the face of the strong evidence presented later (p. 268) that some if not most fish mature as members of the I group, while all II-group fish certainly can be considered mature. It should be mentioned further that segregation on basis of maturity would be expected to be most pronounced at the spawning time, not in midsummer when the cisco is confined in Silver Lake to a narrow stratum of water in the lower part of the thermocline and the upper part of the hypolimnion.

Regardless of the explanation or explanations accepted as to the cause of Lee's phenomenon in the Silver Lake cisco, it appears that the observed discrepancies do not affect the validity of the method used in this paper for the calculation of growth from scale measurements. Nevertheless, there remains the question as to why the phenomenon should be peculiar to the Silver Lake population.

GENERAL GROWTH CURVES FOR THE TROUT LAKE, MUSKELLUNGE LAKE, SILVER LAKE, AND CLEAR LAKE CISCO POPULATIONS

GROWTH IN LENGTH

For each population considered here all collections were combined ⁸ to give a general growth curve (fig. 1). The indicated lengths at the end of the various years of life are in general the grand average of all calculated lengths for these years. In the Trout Lake and Clear Lake ciscoes, however, the irregularities in the later years, that result largely from the small samples, were smoothed in accordance with the observed data on the annual calculated growth increments.

The Silver Lake growth data raise a question as to the value and significance of any "general" growth curve in this population. The presentation of a general growth curve involves the tacit assumption that this curve can be taken to represent the course of growth of an individual that is typical of the population as a whole. However, the Silver Lake growth curve was derived from the combination of several age groups whose growth histories were fundamentally different. It appears characteristic of the Silver Lake cisco that individual growth history and individual life span are definitely correlated. Consequently the combining of all age groups to obtain a general growth curve involves the lumping together of a mass of heterogeneous growth material. The typical individual that such a curve is purported to represent is probably nonexistent. Nor can the growth curve obtained from a single age group be considered homogeneous. A sample of III-group fish, for example, can be expected to contain fish that would normally have died within the year of collection, and along with them others that would have survived to their fifth, sixth, or seventh year, or even longer. All these different groups within a single age group would have different types of growth.

⁸ Certain age groups, however, were eliminated as unreliable because of selection by gear. These were: Trout Lake, all I groups and the II groups of 1930 and 1931; Muskellunge Lake, all I groups; Silver Lake, all I groups. For Clear Lake no groups needed to be eliminated.

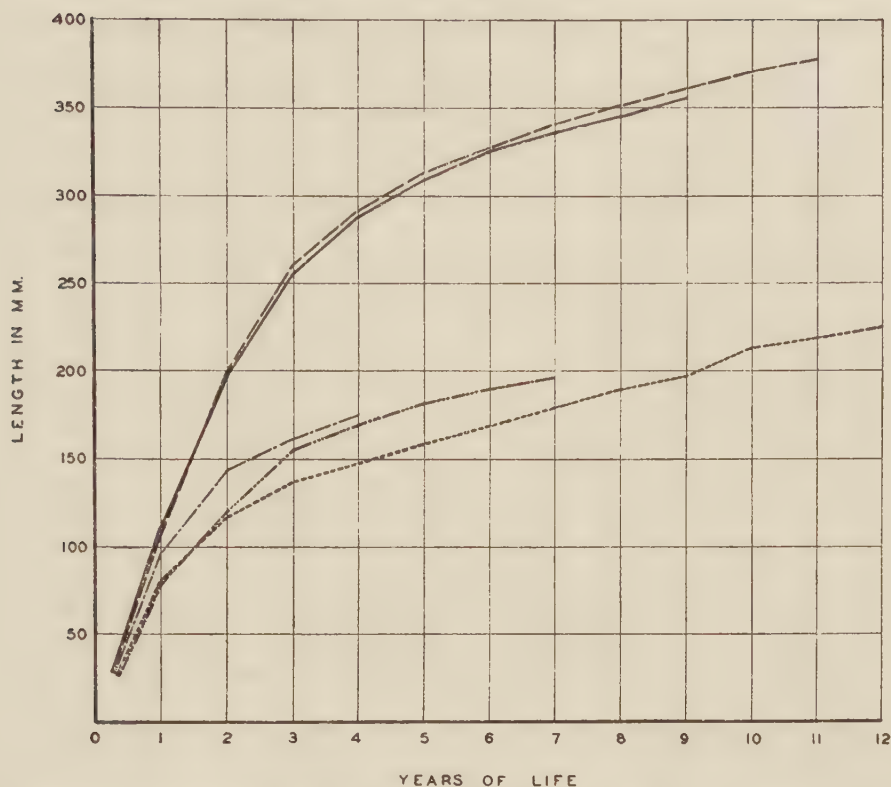


FIGURE 1.—General growth curves showing the average calculated standard length of the cisco (in millimeters) at the end of each year of life. Trout Lake, ---; Muskellunge Lake, — · —; Silver Lake, · · · ·; Clear Lake (males), ———; Clear Lake (females), — — —.

Tables 10 to 14 give for each population the calculated length at the end of each year of life, and the increase, both absolute and percentile, during each year of life. These data are presented graphically in figures 1 to 3.

TABLE 10.—Trout Lake cisco—calculated length in millimeters at end of year, increase in length, and percentage increase in length for each year of life

[All collections combined. Sexes combined]

Number of specimens	Year of life	Length in millimeters	ΔL	$\frac{100\Delta L}{L}$	Number of specimens	Year of life	Length in millimeters	ΔL	$\frac{100\Delta L}{L}$
1	12	225	6	2.7	26	6	168	10	6.3
3	11	219	6	2.8	114	5	158	10	6.8
3	10	213	16	8.1	499	4	148	11	8.0
5	9	197	8	4.2	1,080	3	137	20	17.1
10	8	189	10	5.6	1,182	2	117	36	44.4
14	7	179	11	6.5	1,182	1	81	81	—

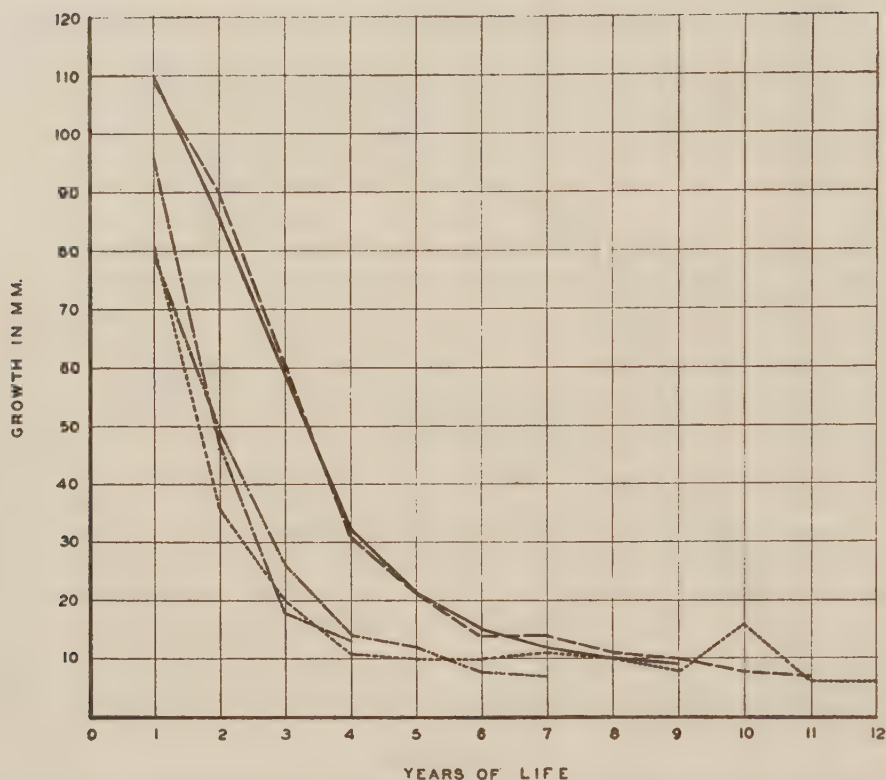


FIGURE 2.—Growth curves showing the increment of growth (in millimeters) in length of the cisco for each year of life. Trout Lake, ---; Muskellunge Lake, —.—; Silver Lake, ...; Clear Lake (males), —; Clear Lake (females), — — —.

TABLE 11.—Muskellunge Lake cisco—calculated length in millimeters at end of year, increase in length, and percentage increase in length for each year of life

[All collections combined. Sexes combined]

Number of specimens	Year of life	Length in millimeters	ΔL	$\frac{100\Delta L}{L}$	Number of specimens	Year of life	Length in millimeters	ΔL	$\frac{100\Delta L}{L}$
2.....	4	174	13	8.1	1,097.....	2	143	47	49.0
373.....	3	161	18	12.6	1,097.....	1	96	96	

TABLE 12.—Silver Lake cisco—calculated length in millimeters at end of year, increase in length, and percentage increase in length for each year of life

[All collections combined. Sexes combined]

Number of specimens	Year of life	Length in millimeters	ΔL	$\frac{100\Delta L}{L}$	Number of specimens	Year of life	Length in millimeters	ΔL	$\frac{100\Delta L}{L}$
1.....	7	196	7	3.7	529.....	3	155	26	20.2
25.....	6	189	8	4.4	564.....	2	129	49	61.2
168.....	5	181	12	7.1	564.....	1	80	80	
397.....	4	169	14	9.0					

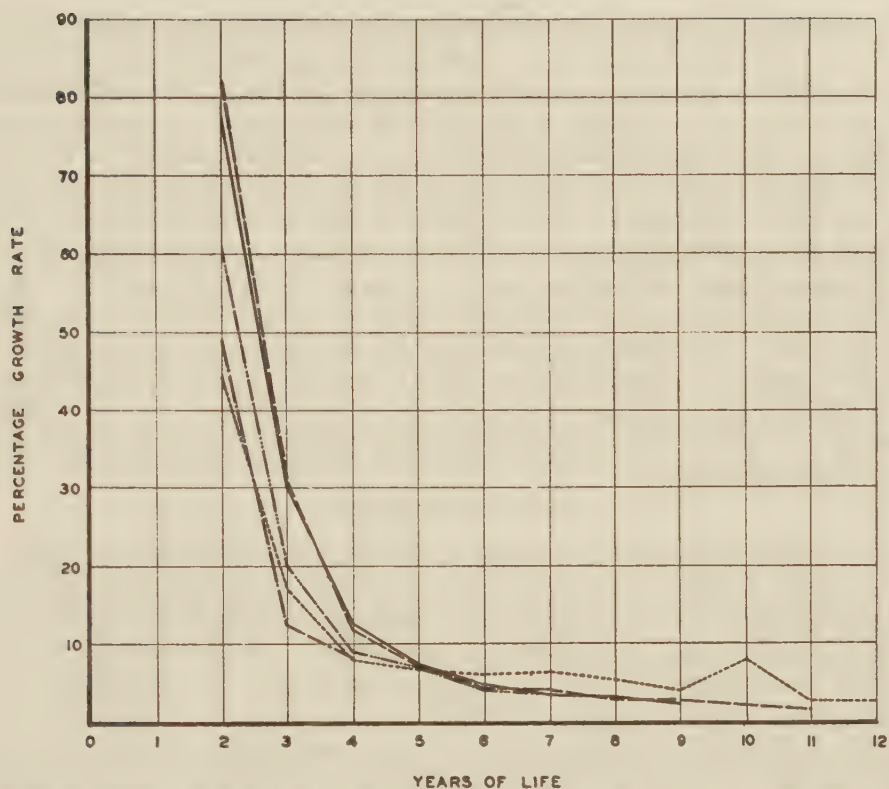


FIGURE 3.—General growth curves showing the percentage increase in length of the cisco in each year of life. Trout Lake, ---; Muskellunge Lake, - . -; Silver Lake, . . . -; Clear Lake (males), —; Clear Lake (females), ---.

TABLE 13.—Clear Lake cisco—males—calculated length in millimeters at end of year, increase in length, and percentage increase in length for each year of life

[All collections combined]

Number of specimens	Year of life	Length in millimeters	ΔL	$\frac{100\Delta L}{L}$	Number of specimens	Year of life	Length in millimeters	ΔL	$\frac{100\Delta L}{L}$
1.....	9	354	9	2.6	73.....	4	287	32	12.5
11.....	8	345	10	3.4	122.....	3	255	59	30.1
28.....	7	335	12	3.7	176.....	2	196	86	78.2
41.....	6	323	15	4.9	216.....	1	110	110	-----
52.....	5	308	21	7.3					

TABLE 14.—Clear Lake cisco—females—calculated length in millimeters at end of year, increase in length, and percentage increase in length for each year of life

[All collections combined]

Number of specimens	Year of life	Length in millimeters	ΔL	$\frac{100\Delta L}{L}$	Number of specimens	Year of life	Length in millimeters	ΔL	$\frac{100\Delta L}{L}$
1.....	11	376	7	1.9	83.....	5	312	21	7.2
4.....	10	369	8	2.2	101.....	4	291	31	11.9
7.....	9	361	10	2.8	147.....	3	280	61	30.7
28.....	8	351	11	3.2	195.....	2	199	90	82.6
61.....	7	340	14	4.3	224.....	1	109	109	-----
74.....	6	326	14	4.5					

In the amount of growth the Clear Lake cisco stands far above the other three populations. The Trout Lake cisco shows the least amount of growth. The Silver Lake fish occupy a position intermediate between the Trout Lake and Muskellunge Lake populations. Examination of the curves showing annual increments and annual percentage increase throws further light on the nature of the growth of the four populations. If the percentage increase is considered to represent the rate of growth, it will be seen that beyond the fourth year of life the growth rates of the four populations show only small differences and that beyond the fifth year the Trout Lake fish, although the smallest in actual size, have consistently the highest rate of growth. The annual growth increments of the populations show no great differences beyond the fifth year of life. These facts indicate that the differences in the size of the adult fish in the four populations depend upon the nature of growth during the early years of life. There is a general convergence of growth rates at the fourth or fifth year of life, but at that time the characteristic nature of the size composition for each population is well established.

GROWTH IN WEIGHT

Tables 15 to 18 present the average weight in grams for each age group in each year's collection, together with summaries for the different years' collections combined, of average weight of each age group, the yearly increments based on the average weights, and the yearly percentage increase in weight. In the consideration of average growth in weight for the different populations the effect of gear selection should be kept in mind for the same age groups (marked with asterisks) that were eliminated in the calculation of the general growth in length (see footnote p. 226). It was found possible to combine the sexes in the Trout Lake and Muskellunge Lake samples, but not in the Clear Lake and Silver Lake collections. The females of the Clear Lake population grow in weight much more rapidly than do the males, while the males from Silver Lake tend toward a slightly better growth than do the females.

TABLE 15.—*Trout Lake cisco*—Average weight in grams of each age group in each year's collection, and grand average weight for each age group, 1928, 1930, and 1931 collections combined, together with the annual increment and the percentage increase

[Sexes combined. The average weights for the I-group fish are probably too high as the result of gear selection; selection probably affected the II-group weight values only slightly. Number of specimens in parentheses. Groups marked with asterisks unreliable because of selective action of gear]

Age	Year of capture			Grand average	ΔW	$\frac{100 \Delta W}{W}$
	1928	1930	1931			
XII.....			172 (1)	172 (1)	-----	-----
XI.....			119 (2)	119 (2)	-----	-----
X.....			111 (2)	111 (2)	-----	-----
IX.....			50 (2)	50 (2)	3	6.4
V.....		54 (9)	45 (23)	47 (32)	6	14.6
IV.....	42 (17)	44 (99)	39 (139)	41 (255)	4	10.8
III.....	37 (61)	37 (347)	36 (129)	37 (537)	6	19.4
II.....	31 (102)	*32 (36)	*33 (50)	31 (102)	-----	-----
I.....	*26 (2)		*27 (2)	*26 (4)	-----	-----

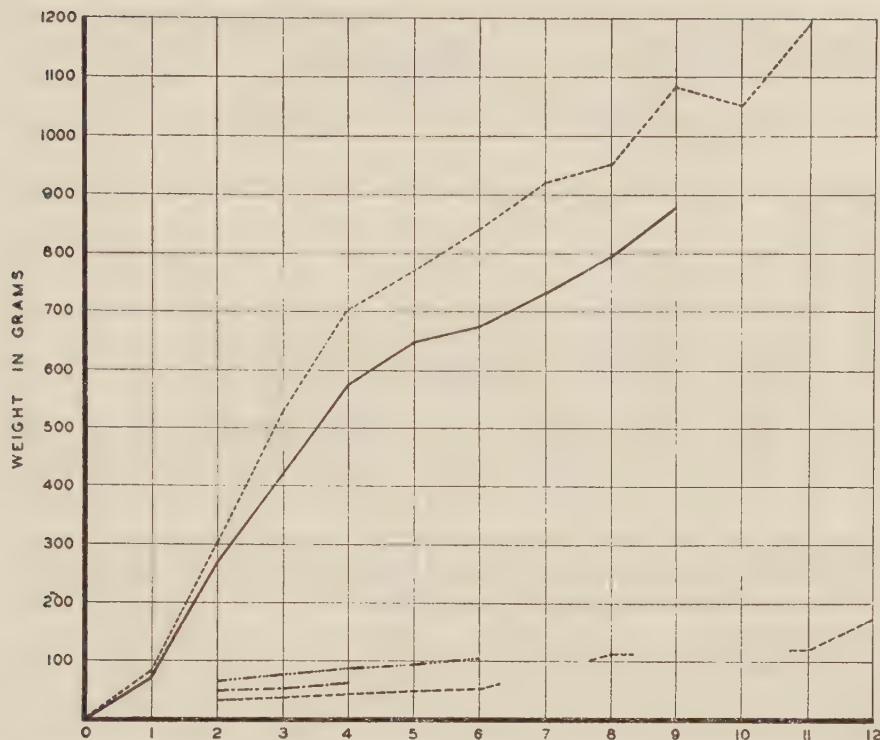


FIGURE 4.—General growth curves showing the average weight (in grams) of the different age groups of cisco at time of capture in summer. Trout Lake, ---; Muskellunge Lake, -.-.-; Clear Lake, — . . . —; Clear Lake (males), —; Clear Lake (females), — — —.

TABLE 16.—Muskellunge Lake cisco—Average weight in grams of each age group in each year's collection, and grand average weight for each age group, 1928, 1930, and 1931 collections combined, together with the annual increment and the percentage increase

[Sexes combined. The average weights for the I-group fish are probably too high as the result of gear selection. Number of specimens in parentheses. Groups marked with asterisks unreliable because of selective action of gear]

Age	Year of capture			Grand average	ΔW	$\frac{100\Delta W}{W}$
	1928	1930	1931			
IV			60 (2)	60 (2)	9	17.6
III	55 (10)	49 (14)	51 (266)	51 (290)	5	10.9
II	50 (252)	45 (214)	42 (229)	46 (695)		
I	*33 (19)	*39 (17)	*31 (9)	*35 (45)		

TABLE 17.—Silver Lake cisco—Average weight in grams of each age group in each year's collection, and grand average weight for each age group, for the 1930 and the 1931 collections combined, together with the annual increment and the percentage increase

[Sexes separately. The average weights for the I-group fish are probably too high as the result of gear selection. Number of specimens in parentheses. Groups marked with asterisks unreliable because of selective action of gear]

Age	Year of capture					Grand average		ΔW		$\frac{100\Delta W}{W}$	
	1928	1930		1931							
	Male and female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
VI			106 (3)		104 (8)		104 (11)		11		11.6
V	81 (10)	98 (10)	99 (15)	95 (12)	92 (22)	96 (22)	95 (37)	10	11	11.6	13.1
IV	68 (69)	86 (23)	87 (35)	86 (13)	80 (22)	86 (36)	84 (57)	4	11	4.9	15.1
III	59 (46)	86 (13)	74 (12)	76 (10)	73 (13)	82 (23)	73 (25)	16	12	24.2	19.7
II	50 (9)	68 (3)	64 (4)	64 (4)	60 (8)	66 (7)	61 (12)				
I	*28 (1)			*32 (24)	*35 (25)	*32 (24)	*35 (25)				

TABLE 18.—*Clear Lake cisco*—Average weight in grams of each age group in each year's collection, and grand average weight for each age group, for the 1931 and the 1932 collections combined, together with the annual increment and the percentage increase

[Sexes separately. Number of specimens in parentheses]

Age	Year of capture				Grand average		ΔW		$\frac{100\Delta W}{W}$	
	1931		1932							
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
XI				1,190 (1)		1,190 (1)				12.1
X		1,035 (1)		1,090 (1)		1,062 (2)		128		-2.1
IX		915 (1)	880 (1)	1,170 (2)	880 (1)	1,085 (3)	84	135	10.6	14.2
VIII	760 (3)	937 (11)	811 (7)	969 (8)	796 (10)	950 (19)	67	33	9.2	3.6
VII	718 (6)	859 (17)	737 (9)	1,000 (12)	729 (15)	917 (29)	56	76	8.3	9.0
VI	687 (7)	844 (8)	625 (2)	820 (1)	673 (9)	841 (9)	26	71	4.0	9.2
V	710 (2)	740 (1)	629 (7)	774 (7)	647 (9)	770 (8)	69	65	11.9	9.2
IV	603 (5)	756 (7)	567 (11)	680 (14)	578 (16)	705 (21)	160	175	38.3	33.0
III	413 (17)	525 (19)	422 (23)	534 (21)	418 (40)	530 (40)	151	230	56.6	77.7
II	272 (28)	303 (27)	259 (20)	295 (13)	267 (43)	306 (40)	196	220	276.1	275.0
I	75 (18)	88 (15)	68 (20)	70 (11)	71 (38)	80 (26)				

The weight data are based on fewer specimens than are the length data since most of the fish that were preserved for morphometric study were not weighed in the field and therefore were not used in these studies.

Examination of the data bearing on growth in weight reveals how sharply the growth of the Clear Lake cisco differs from that in the other three populations (fig. 4). The differences that exist among the populations depend upon differences in the length-weight relationships in the various populations as well as upon differences in the amount of growth in length. The questions of form and changes in form, and of the relationship between length and weight are considered in a separate section (pp. 237-247.)

COMPARISON OF THE GROWTH OF THE TROUT LAKE, MUSKELLUNGE LAKE, SILVER LAKE, AND CLEAR LAKE CISCO POPULATIONS WITH THAT OF CISCO POPULATIONS IN OTHER REGIONS

Data on the growth of the cisco or lake herring have been published for Lake Erie by Clemens (1922), for Oconomowoc and Pine Lakes in southern Wisconsin by Cahn (1927), for Lake Huron by Van Oosten (1929), for Lake Ontario by Pritchard (1931), for the Indian Village Lakes in northern Indiana by Hile (1931), and for Hudson Bay by Dymond (1933). Tables 19 and 20 present a comparison of the growth of these populations with that of the populations of the present investigation. The lengths (table 19) are expressed in millimeters, the weights (table 20) in grams, and the ages in both tables as the number of years of life completed. The methods of presentation of the various authors were altered to conform to this uniform method of expressing length, weight, and age. Dymond did not include data on growth in weight of the Hudson Bay cisco. The largest fish in his collection was a female, 383 millimeters long and weighed 793 grams.

TABLE 19.—*Comparison of growth in length, expressed in millimeters, of 11 cisco populations*

[The data for the 6 lakes at the right were adapted from various authors as indicated in the text]

Age	Trout ¹	Muskel- lunge ¹	Silver ¹	Clear ¹		Huron ²	Ontario ³	Erie ³	Indian Village ³	Ocono- mowoc ⁴	Pine ⁴	Hudson Bay ³
				Male	Fe- male							
XII	225											
XI	219				376							
X	213				369							
IX	197			354	361		345			386	345	
VIII	189			345	351	292	303	285		374	338	
VII	179		196	335	340	274	297	275	374	362	330	336
VI	168		189	323	326	258	270	255	336	315	283	308
V	158		181	308	312	244	253	235	342	282	246	290
IV	148	174	169	287	291	235	233	215	316	223	195	284
III	137	161	155	255	260	218	226	190	301	174	162	214
II	117	143	129	196	199	185	196	160	260	135	125	184
I	81	96	80	110	109	127	129	125				

¹ Calculated lengths at the end of the year of life indicated.² A combination of calculated lengths and actual lengths measured in November.³ Actual measured lengths at time of capture during the growing season. The ages of the fish are really greater than indicated here.⁴ Actual measured lengths in midwinter after the completion of the growing season.TABLE 20.—*Comparison of growth in weight, expressed in grams, of 10 cisco populations*

[The data for the 6 lakes at the right were adapted from various authors as indicated in the text]

Age	Trout	Muskel- lunge	Silver		Clear		Huron	Ontario	Erie	Indian Village	Ocono- mowoc	Pine
			Male	Fe- male	Male	Fe- male						
XII	172											
XI	119					1,190						
X						1,062		666			696	436
IX					880	1,085		751			623	406
VIII					796	950		454	354		611	343
VII	111				729	917		488	269	810	527	282
VI	50			106	673	841	221	303	213	782	445	190
V	47		96	95	647	770	175	216	156	648	366	120
IV	41	60	86	84	578	705	159	181	128	523	257	85
III	37	51	82	73	418	530	143	159	85	462	166	60
II		46	66	61	267	306	100	105		278	105	45
I					71	80		31				

It should be mentioned that the length data of table 19 are not in all cases strictly comparable from one population to another. The data for Trout, Muskellunge, Silver and Clear Lakes are all calculated lengths; the data for Lake Huron are a combination of calculated lengths and actual lengths measured in November; the data for Lake Ontario, Lake Erie, the Indian Village Lakes, and Hudson Bay represent actual measurements of fish caught during the growing season; and the data of Oconomowoc Lake and Pine Lake are actual average measurements of fish taken in the winter after the close of the growing season. These small differences in the manner of presentation should not affect the value of the data for purposes of comparison.

Though growth in length of the cisco varies widely in different localities, certain consistent likenesses as to the manner of growth are apparent. The greatest growth in length occurs in the first year of life. The growth of the second year is large but less than that of the first. Growth decreases markedly in the third year of life. Throughout the later years the annual increment of growth in length tends to remain fairly constant. Growth in weight is too greatly complicated by the questions of differences in form and of change of form to permit a general description of the style of growth with respect to this character.

Willer (1929) called attention to the fact that certain fishes can be said to possess a typical species growth curve that retains a characteristic form regardless of the extent to which external factors influence the actual amount of growth. With respect to growth in length the cisco seems to possess such a species growth curve.

It will be noticed in table 19 that the populations showing the greatest (Clear Lake, Indian Village Lakes) and the least (Trout Lake) amount of growth are found in small, inland lakes. Such a situation might be expected in view of the greater diversity of habitat furnished by the smaller bodies of water. The growth in the different populations cannot be classified according to latitude or region, but rather, the differences in growth seem to depend upon purely local conditions within the individual lake or possibly upon the genetic make-up of the local stock.

A population showing a greater amount of growth in length than another does not necessarily show a greater amount of growth in weight. Two examples will illustrate this situation. (See tables 19 and 20.) At all ages beyond the seventh year the Oconomowoc Lake cisco is longer than either the males or females of the Clear Lake cisco, and yet at all ages the weights of the Oconomowoc fish are less than those of the Clear Lake fish of corresponding age. Secondly, at the age of 7 years the weights of the Clear Lake and the Indian Village Lakes ciscoes are approximately equivalent. At the same time the length of the Indian Village Lakes fish at the age of 7 years is greater than that attained by the Clear Lake⁹ males in the ninth year and equal to the length reached by the Clear Lake females in the tenth or eleventh year. These discrepancies between growth in length and growth in weight find their origin in the different length-weight relationships in the various populations. Populations may differ both as to general body form itself and as to the manner of change of form with increase in length.

RANGE OF LENGTH IN INDIVIDUAL AGE GROUPS; MAXIMUM LENGTH AND WEIGHT

Tables 21 to 25 show for the four lakes under consideration here the length distribution of the different age groups in each year's collection. On the whole, length is a poor index of age. The amount of overlap between consecutive age groups is so great that in most instances a fish of a given length might have any of several different ages. This is particularly evident in the Trout Lake data of table 21. In the rapidly growing Clear Lake population, however, the positions of both sexes of the first three age groups (I, II, and III) stand out clearly in the length frequencies. In the 1931 Silver Lake collection the I group is well separated from the remainder of the sample. The Muskellunge Lake collection of 1931 shows a fairly distinct separation of the II and III groups, but a greater abundance of other age groups in the collections of this year might have obscured this division.

⁹ The average lengths of the Clear Lake fish measured at the time of capture were: IX group, male, 355 millimeters; X group female, 377 millimeters; XI group, female, 378 millimeters.

TABLE 21.—Length frequencies (5-millimeter intervals) of each age group of the Trout Lake cisco in each year's collection

Length	I		II			III			IV			V		VI	VII	VIII	IX	XI	XII
	1928	1930	1928	1930	1931	1928	1930	1931	1928	1930	1931	1930	1931	1931	1931	1931	1931	1931	1931
225 to 229																			1
220 to 224																			
215 to 219																		1	
210 to 214																			
205 to 209																			
200 to 204																			
195 to 199																1	1	1	
190 to 194																1	2		1
185 to 189												1				1	1		
180 to 184																1	1		
175 to 179												1		3					
170 to 174												1		1	1				
165 to 169														6	2				
160 to 164														4	3	2			
155 to 159														2	29	1			
150 to 154															1	1			
145 to 149			2	13	2	15	94	41	5	15	98			8	1				
140 to 144			9	6	18	30	70	67	5	2	46								
135 to 139			30	6	18	12	12	42	1		16			3					
130 to 134		1	43	4	15	1	2	12			3								
125 to 129	2		16	4	8			1											
120 to 124		1	2	1															
Average	128	128	134	140	136	143	149	142	147	156	148	167	156	165	175	192	200	205	226

TABLE 22.—Length frequencies (5-millimeter intervals) of each age group of the Muskellunge Lake cisco in each year's collection

[The 1932 III and IV groups are not included because of the high degree of uncertainty in their separation]

Length	I				II				III			IV
	1928	1930	1931	1932	1928	1930	1931	1932	1928	1930	1931	1931
180 to 184					1				2			3
175 to 179					3	4			1			13
170 to 174					14	14			2	4		73
165 to 169					28	46	3		2	5		126
160 to 164					88	92	20	8	3	4		111
155 to 159					78	35	24	6		1		20
150 to 154					27	18	60	7				1
145 to 149					12	5	93	1				
140 to 144					6		50	1				
135 to 139					1		5					
130 to 134					5		3					
125 to 129					8	1						
Average	137	148	136	140	160	162	149	156	172	166	166	176

TABLE 23.—Length frequencies (5-millimeter intervals) of each age group of the Silver Lake cisco in each year's collection

Length	I		II			III			IV			V			VI		VII
	1928	1931	1928	1930	1931	1928	1930	1931	1928	1930	1931	1928	1930	1931	1930	1931	1931
205 to 209													2				
200 to 204									1			1	6		1	5	1
195 to 199						1	2	1		13	13	1	5	13	2	4	
190 to 194							6	3	12	22	2	7	26			8	
185 to 189							6	6	19	37	4	2	21			4	
180 to 184			1	1			1	20	19	6	17		14				
175 to 179				6			5	2	19	6	10	2					
170 to 174				6			9	19	24	6							
165 to 169			2	3			12	1	8	12	2						
160 to 164			2				15		1	4							
155 to 159		2	1				8										
150 to 154		3	3					1									
145 to 149		14															
140 to 144		21	1														
135 to 139		17															
130 to 134		5															
125 to 129																	
120 to 124		1															
Average	133	141	157	173	171	165	181	177	174	183	183	182	193	188	197	194	201

TABLE 24.—Length frequencies (10-millimeter intervals) of each age group of the Clear Lake cisco (males) in each year's collection

Length	I		II		III		IV		V		VI		VII		VIII		IX
	1931	1932	1931	1932	1931	1932	1931	1932	1931	1932	1931	1932	1931	1932	1931	1932	1932
360 to 369																	2
350 to 359									1								1
340 to 349											3		1	5	1		1
330 to 339							2	1	2	1			5	1	2		1
320 to 329								3	1	3	2	2		2			2
310 to 319					1	2	6	4	1	1	5			1			
300 to 309					1	2	2	2	1								
290 to 299					10	10											
280 to 289					8	4											
270 to 279			5	1	3	4		1									
260 to 269			5	8	3												
250 to 259			14	4		1											
240 to 249			5	5													
230 to 239			3	1													
220 to 229			1														
210 to 219	1		1	1													
200 to 209	1																
190 to 199	1																
180 to 189	4	5															
170 to 179	8	10															
160 to 169	5	5															
Average	178	176	253	254	285	290	317	314	325	320	326	320	331	336	338	345	355

TABLE 25.—Length frequencies (10-millimeter intervals) of each age group of the Clear Lake cisco (females) in each year's collection

Length	I		II		III		IV		V		VI		VII		VIII		IX		X		XI
	1931	1932	1931	1932	1931	1932	1931	1932	1931	1932	1931	1932	1931	1932	1931	1932	1931	1932	1931	1932	1932
380 to 389														2					1		
370 to 379													2	2							
360 to 369													3	2	3				1		1
350 to 359									1	4	1		3	3	7	5	1	1			
340 to 349							1	2	1	4	4		7	3	1						
330 to 339							2	6	2	3	2				1						
320 to 329						2	1	3	1		2	1	3								
310 to 319					5	9					2		1								
300 to 309					8	10															
290 to 299			1		6	1															
280 to 289			3		4																
270 to 279			6	4	4																
260 to 269			11	2		1															
250 to 259			10	7																	
240 to 249			3																		
230 to 239			1																		
220 to 229																					
210 to 219																					
200 to 209	4																				
190 to 199	1	1																			
180 to 189	8	2																			
170 to 179	5	7																			
160 to 169																					
150 to 159			1																		
Average	186	176	264	262	302	308	334	329	338	342	339	320	344	362	354	356	351	368	376	379	378

There are some disagreements between the length distributions of fish of the same age, but taken in different seasons. Some of these differences, particularly in the younger age groups, are due to the variation in the time of the collection of the sample within the growing season. The I groups of Clear Lake will serve as an example. (See tables 24 and 25.) In 1932 these ciscoes were collected from July 12 to July 19, while in 1931 they were taken during two periods, July 22 to July 28 and September 3 to September 5. Since the September samples averaged more in length (the average length of the September fish was about 200 millimeters) than the July samples, their presence accounts for the greater upward extension of the length distribution of the 1931 I-group Clear Lake ciscoes. However, at least some

of the other differences between the length distributions of fish of the same age may be accounted for by the actual differences in the growth histories of the year classes they represent. This appears to be true, for example, in the II groups from Muskellunge Lake (table 22). The 1931 II-group fish from this lake were much smaller in average size than those of the preceding 2 years. The examination of the tabulation of calculated lengths for these various groups (table 4) likewise shows that the 1931 II group (1929 year class) actually grew less during the first and second years of life than did the 1929 and 1930 II groups (year classes of 1927 and 1928).

In table 26 are given the data relative to the longest and the heaviest fish taken from each population. (Data concerning the lengths and weights of the oldest fish taken may be obtained from tables 3 to 7.) There is sufficient variation in individual growth that the largest individual need not necessarily be the oldest. In the Silver Lake collections and for both sexes of the Clear Lake samples the largest fish are from 1 to 4 years below the observed maximum age. It is true further that the largest fish with respect to length is not always the heaviest (for example, see the data on the longest and the heaviest fish from Silver Lake). The differences among the maximum sizes attained in the different populations are more striking if size is considered in terms of weight. The Clear Lake fish reach a weight approximately 17 times as great as those from Muskellunge Lake, 10 times as great as those from Silver Lake, and 7 times as great as those from Trout Lake.

TABLE 26.—*Data concerning the longest and the heaviest cisco in each of the 4 lakes*

Lake	Year of capture	Age	Length in millimeters	Weight in grams	Sex
Trout.....	1931	XII	226	172	Female.
Muskellunge.....	1932	IV	180	70	Do.
	1932		¹ 188		Male.
Silver.....	1930	V	206	110	Female.
	1930	VI	204	120	Do.
	1932	VIII	368	910	Male.
Clear.....	1931	X	¹ 388		Female.
	1932	VII	383	1,210	Do.

¹ This fish was not weighed before it was preserved. The length recorded includes a correction for shrinkage.

The maximum size attained depends both upon rate of growth and upon the maximum age of survival. The Trout Lake cisco is the slowest growing of the four populations, yet a few individuals survive to such an age as to reach a size greater than is attained by the fish in either Silver or Muskellunge Lakes. It is probable that further collections might change the order of arrangements of the lake with respect to the maximum size reached by the cisco, as well as the absolute maximum values for length and weight.

CONDITION AND THE RELATIONSHIP BETWEEN LENGTH AND WEIGHT

Weight in fishes may be considered a function of the length. If form and specific gravity ¹⁰ were constant throughout life the relationship could be expressed by the equation,

$$W = cL^3, \quad (1)$$

where

W = weight,

L = length,

and

c = constant.

The above equation is a statement of the well-known cube law. Actually, in nature, the value of c is not constant for a species or population but is subject to a

¹⁰ Reibisch (1908) could find no appreciable seasonal variation in the specific gravity of the plaice. Keys (1928) pointed out that the hydrostatic equilibrium that exists between the fish and its environment renders great fluctuations in specific gravity unlikely.

wide range of variation. The values of c under various definitions (coefficient of condition, condition factor, length-weight factor) have been used widely by fisheries investigators as measures of individual or average seasonal and regional differences in the condition or "degree of well-being" of fishes. Some investigators have used the coefficient as a measure of the state of sexual development. Others have considered condition to apply only to the state of nourishment and have removed the gonads before taking the weight for the calculation of the coefficient. Yet others have used the coefficient merely as a measure of relative heaviness and have recognized the effect of both the state of sexual development and of the state of nourishment on the determination of its value.

In addition to its use as a means of estimating condition, the equation (1) has been employed also to describe the general length-weight relationship in populations of fishes, and thus serve as the basis for the calculation of unknown weights of fish of known length or of unknown lengths of fish of known weight. The use of the equation in this latter capacity has met with indifferent success, due to the failure of the cube law to describe accurately the relationship of length to weight in many forms of fishes. Fulton (1904) who applied the law to the relationship of length to weight in several marine species stated:

The law in regard to the increase in weight according to the cube of the length, although broadly true, does not accurately apply in the case of the fishes examined. With scarcely an exception, the weight at a given length is greater than the weight calculated from the law, so that if the specific gravity of the fishes remains constant they must increase somewhat more in other dimensions than in length

Although the cube law does appear to apply to the length-weight relationship in some species (Crozier and Hecht, 1914; Hecht, 1916), these instances appear to be the exceptions, for the observations of Fulton in regard to the inadequacy of the cube law in describing the length-weight relationship in fishes have been repeated by numerous investigators and on many forms of fishes. In recent years a much more satisfactory method of describing the length-weight relationship in fishes has been developed through the use of the more general equation:

$$W = CL^n, \tag{2}$$

where W =weight,
 L =length,
and c =constant.

In this equation the values of both C and n are determined empirically.

Such a relationship has been determined by Järvi (1920), Tjurin (1927), Clark (1928), Keys (1928), Fraser (1931), Hart (1931, 1932), Tester (1932), Walford (1932), and Schultz (1933).

Some of the above authors have, however, confused the two entirely distinct issues of describing condition and expressing the length-weight relationship, and have abandoned the use of coefficients of condition based on the cube relationship in favor of those based on an empirically determined exponent (C in $W = CL^n$). That coefficients calculated from the cube relationship and from empirically determined exponents are in no sense of parallel significance as measures of condition appears from the following simple illustration.

A fish with a length of 1 foot and a weight of 1 pound will show on the basis of the cube relationship a coefficient of condition of 1.00. In conformity with a rather general usage this quantity may be designated as K . If this fish doubles its length without change of form or of specific gravity its weight at the length of 2 feet will be 8 pounds, and the value of K will continue to be 1.00. If, however, the weight at 2 feet is 10 pounds instead of 8 the value of K at this greater length will be 1.25, and it will be known that a change of form¹¹ has occurred along with growth in length. It may be considered that 2 pounds of the weight of this 10-pound fish represent its change of form; this change is measured directly in the increased value of K . The 10-pound fish is 25 percent heavier than the 8-pound fish and is 25 percent *relatively* heavier than the 1-pound fish (that is, the 10-pound fish corresponds in form to a fish that would have a weight of 1.25 pounds at the length of 1 foot). Thus it may be seen that values of K , by reason of their calculation from the cube relationship are direct and quantitative measures of form or relative heaviness, and in this sense are directly comparable between fishes of any length.

Now if the weights of 1 pound at the length of 1 foot and of 10 pounds at 2 feet were to represent actual average conditions within a population, the corresponding length-weight equation would be:

$$W=1.00L^{3.32193}$$

The coefficients of condition calculated from this higher empirical exponent are 1.00 both for the fish at the length of 1 foot and weight of 1 pound and for the fish at the length of 2 feet and weight of 10 pounds. Thus it may be seen that the coefficient C fails entirely to measure in any way the change of form that occurred with increase in length. Further, the value of C for a fish that weighs 8 pounds at the length of 2 feet is 0.80, and from this value it would appear that a fish that doubles its length without change of form actually suffers a loss of condition. Since the assumption is hardly tenable that a fish can suffer such a great loss of condition without undergoing any change of form or relative heaviness it must be concluded that values of C calculated from empirically determined exponents fail to serve as satisfactory measures of condition. Questions concerning the use of C as a coefficient of condition will receive further consideration in connection with the presentation of the data of this investigation on condition and the length-weight relationship in the cisco populations of Trout Lake, Muskellunge Lake, Silver Lake, and Clear Lake. At the present time, however, a brief review will be presented of the observations and opinions of authors who have used or suggested the use of C in equation (2) as a coefficient of condition.

The observations of Järvi (1920) should be included in this review, although in justice to that author it should be emphasized that he was concerned primarily with the calculation of unknown lengths and weights from a general length-weight relationship rather than with the measure of condition. Järvi's data are of particular interest here since he included a comparison of coefficients based on the cube relationship and as determined from equations of the type, $W=CL^n$, with empirically determined exponents. His coefficients for the males, the ripe females, and the spent females of the kleine Maräne (*Coregonus albula*) were, on the basis of the cube relationship,

¹¹ The term "form" as employed throughout this section carries with it no implications as to details of shape, but refers only to relative heaviness of stature.

0.00848, 0.00989, and 0.00830, respectively.¹² The coefficients as calculated from formulas with empirically determined exponents were, for the males, ripe females, and spent females, 0.0050, 0.0020, and 0.0056, respectively. The exponents in these last three formulas were 3.2 for the males, 3.64 for the ripe females, and 3.16 for the spent females. The comparison of the coefficients derived by the two methods shows clearly that those based on empirical exponents fail completely to reflect the relative heaviness of the fish groups to which they pertain. While the values of K based on the cube relationship show that the ripe females are on the average the relatively heaviest group, followed in order by the males and the spent females, the values of the coefficients calculated from equations with empirical exponents follow exactly the reverse order. Thus on the basis of the values of C of equation (2) the relatively heaviest group of fish would appear to be in the poorest condition. If the values of the two types of coefficients are compared in relation to the values of the exponents, n , it appears that while the values based on the cube relationship depend on the relative heaviness of the fish upon which they are based, the values of the coefficients calculated from equations with empirical exponents depend primarily not on the heaviness of the fish but rather on the value of the exponents. A large value of n is associated with a small value of the coefficient—and the reverse.

Clark (1928) appears definitely to have confused the two problems of describing condition and expressing the length-weight relationship. From her study of condition and the length-weight relationship in the California sardine (*Sardina caerulea*) Clark concluded: "The weight of sardines increases at a rate slightly greater than the cube of the length. For the data studied the correct formula for the weight-length factor was found to be $F = \frac{1000 W}{L^{3.15}}$. But for the purpose of the present study the formula $F = \frac{1000 W}{L^3}$ was sufficiently accurate."

Clark evidently believed that the coefficient of condition (weight-length factor), to be accurate, should tend to hold a constant value at all lengths of the fish, for she stated: "The more a species departs from this general weight-length relationship [cube relationship], the greater the error involved in the factor." Concerning the changes in the value of the factor with increasing length she observed further: "Due to the error introduced from calculating F on the basis of the cube of the length, the curve resulting from the equation $F = \frac{1000 W}{L^3}$ rises consistently throughout the range of sizes represented in the commercial catch at San Pedro."

Clark's conclusion that the failure of the cube law to describe the length-weight relationship makes inaccurate the use of coefficients of condition (weight-length factors) based on the cube relationship is scarcely justifiable, particularly in view of the fact that coefficients based on empirical exponents fail to reflect differences in form or relative heaviness while those based on the cube relationship offer a direct measure of relative heaviness independent of general length-weight relationships and comparable as measures of relative heaviness between fish of any length. Clark actually studied variations in the weight-length factor on the basis of values calculated from the cube relationship, but did so only because she considered that the use of these values introduced "only a minor error into the work."

¹² In the data from which these coefficients were determined weights were recorded in grams and lengths in centimeters.

Clark's data on the correlation between weight-length factors (calculated from the cube relationship) and the fat content of the sardine offers convincing evidence that measures of condition should be calculated from the cube relationship. Her data show conclusively that variations with length in the value of the weight-length factor are reflected closely in corresponding variations with length in the fat content of the sardine. Inasmuch as relative heaviness is thus showed to be dependent on fatness (condition), changes with length in relative heaviness must be considered also to represent changes of condition. In view of this fact it does not appear valid to measure condition in terms of a quantity that tends to be constant for fish of all lengths regardless of actual changes that may occur in relative heaviness of form with change in length. Since the quantity C in the equation $W=CL^3$ tends toward this constancy and fails to measure relative heaviness it must fail also to measure the differences of fatness (condition) upon which differences in relative heaviness depend.

Tester (1932) likewise appears to have confused the two problems of measuring condition and describing the general length-weight relationship. Concerning his method of determining the general length-weight relationship in the smallmouth black bass (*Micropterus dolomieu*) he stated:

Following the method used by Hart (1931) and others the relationship between length and weight for bass from Perch Lake [Ontario] was obtained by plotting average lengths against average weights on double logarithmic paper and deriving the natural slope of the resultant straight line drawn through the points. It was found that the weight increased by the power 3.1(7) of the length. * * *

Tester assumed, however, that the failure of the cube law to describe the length-weight relationship made the use of coefficients of condition based on the cube relationship invalid. Concerning the equation, $K = \frac{100 W}{L^3}$, employed by Hile (1931) to describe condition in several species of Indiana lake fish, Tester stated:

This equation is only approximate and might be better expressed—

$$K = \frac{100 W}{L^x}$$

In the case of the Perch Lake bass the power x would have a value 3.1(7). If the power $x=3$ is used, the value of K tends to increase with the length of the fish whereas it should remain constant.

Tester used the value $x=3.1(7)$ as determined from the Perch Lake bass to compute coefficients of condition for his smaller samples from Phantom Lake, Lake Nipissing, and Georgian Bay, but observed that, "To be strictly accurate, the value x should be determined separately for each of the latter three bodies of water. * * *"

Had Tester actually determined the value of the exponent for each of the bass populations he studied he would probably have become aware of the difficulties involved in the use of coefficients of condition based on empirical exponents.

Schultz (1933) expressed the relationship of length to weight in the bay smelt (*Atherinops affinis oregonia*) by the equation $W=FL^{2.69}$. He also employed the quantity F as a measure of seasonal changes in weight, dependent on the state of development of the gonads. That Schultz considered the length-weight factor, F , identical in significance with factors calculated from the cube relationship is apparent from the following statement: "The length-weight factor, F , was used to estimate the state of development of the gonads, as has been done by D'Arcy Thompson (1917),

Van Oosten (1929), Clark (1928b), Weymouth (1918 and 1923), Reibisch (1911), Crozier and Hecht (1915), and others.¹³

Of the above authors some employed the cube relationship in the study of the length-weight relationship (Thompson, Van Oosten, Weymouth (1918), Crozier and Hecht), while others used empirical exponents (Clark, Weymouth (1923)).

Because of the serious objections to the use of coefficients of condition based on empirical exponents, condition in this investigation has been measured by coefficients calculated from the cube relationship. The comparison of the equations $W=KL^3$ and $W=CL^n$ reveals an interesting connection between condition and length in populations that deviate from the cube relationship. The equation, $W=CL^n$, may be written in the form:

$$W=f(L) \cdot \phi(L), \quad (3)$$

where

$$\begin{aligned} f(L) &= CL^m, \\ \phi(L) &= L^3, \end{aligned}$$

and

$$m=n-3.$$

Thus it may be seen that where weight can be expressed as a parabolic function of the type $W=CL^n$ condition can be expressed by a similar function of length. While this definition of condition as a function of length is valid only insofar as the equation (3) actually describes the length-weight relationship, the failure of equation (3) has no effect on the value of coefficients calculated from the cube relationship as measures of relative heaviness. Where the coefficient of condition does behave as a parabolic function of length (hyperbolic if $m < 0$), the value of $m=n-3$ measures the rate of change of form or condition.¹⁴

In order to have the most complete data for the study of condition the value of $f(L) = \frac{W}{L^3}$ was calculated for each individual specimen. Since lengths were recorded

¹³ This statement of Dr. Schultz as it pertains to the studies of other investigators is in some points inaccurate. Van Oosten made no use of the coefficient of condition to study the state of sexual development but was interested primarily in deriving a general length-weight equation; he did, however, quote Thompson (1917) as to the effect of sexual state on the value of the coefficient. Clark used the weight-length factor chiefly as a measure of the state of nourishment or fatness as the following statement shows: "The monthly and yearly fluctuations in the weight-length factors of sardines were due, therefore, to some changes in the composition of the body tissue of the fish, presumably an increase or decrease in the fat content, and not to the amount of food in the alimentary tract, or to the growth of the sex organs." Weymouth (1918 and 1923) was concerned with the general length-weight relationship and not with any individual or seasonal fluctuations in the length-weight factor. Reibisch's coefficient was calculated neither from $W=KL^3$ nor $W=CL^n$, but was a "Dickenkoeffizient" with the formula $\delta = \sqrt{\frac{40000}{L^3} \cdot \frac{G}{L}}$, (G =weight in grams, L =length in centimeters). Reibisch discussed the effect of sexual state on the state of nourishment, but, in order to make δ describe only the state of nourishment, removed the gonads before weighing. Crozier and Hecht were concerned with the determination of a general length-weight equation. They stated: "All the fish examined (over 400) were either spent or unripe; so we are sure that none of the weights recorded are influenced by the ripening of the gonads." (The date of issue of Crozier and Hecht's paper was 1914, not 1915.)

¹⁴ The differential equations corresponding to the equations $W=CL^n$, and $f(L)=K=CL^m$ are:

$$\begin{aligned} \frac{dW}{W} &= n \frac{dL}{L}, \\ \text{and} \\ \frac{dK}{K} &= m \frac{dL}{L}. \end{aligned}$$

Now $\frac{dW}{dt} \cdot \frac{1}{W}$, $\frac{dL}{dt} \cdot \frac{1}{L}$, and $\frac{dK}{dt} \cdot \frac{1}{K}$, where t =time, are the relative rates of change in weight, length, and condition, respectively. The exponent n describes the ratio of the relative rates of change of weight and length, while m describes the ratio of the relative rates of change of condition (form) and length. If $n=3$, $m=0$, and growth proceeds without change of form. If $n \neq 3$, then $m \neq 0$, and the values of the exponents measure the rate of change of form.

in millimeters and weights in grams, the actual values of $f(L)$ were quite small. To avoid the use of such small decimals the coefficient of condition K as actually used was defined:

$$K=f(L) \times 10^5 \quad (4)$$

In the Trout Lake, Muskellunge Lake, Silver Lake, and Clear Lake populations the variation of condition with length, and of weight with length conforms closely over certain length intervals with the conditions defined by equation (3). Consequently it was possible to determine equations describing condition and weight as functions of length by fitting parabolic equations to the observed average values of K at different lengths.

The assumed relationship between K and L indicates a linear relationship between the logarithms of their values:

$$\log K=a+m \log L, \quad (5)$$

where

$$a=\log C+5.$$

It is possible to determine the values of C and m by fitting a straight line to the logarithms of corresponding values of K and L . The determined values of C and m can be used in writing not only the equation for K as a function of length but also for writing the equation for weight as a function of length.¹⁵

Table 27 contains the equations obtained for $K=C \times 10^5 L^m$ and $W=CL^n$. The data from which the equations were determined are found in tables 28 to 31. The tables mentioned last contain also a comparison of actual weights with theoretical weights calculated from the length-weight equations of table 27.

TABLE 27.—Equations for $K=C \times 10^5 L^m$ and $W=CL^n$ as determined for the various cisco collections

Lake	Year of collection	Sex	Number of specimens	Range of L	$K=C \times 10^5 L^m$	$W=CL^n$
Trout.....	1928	♂, ♀	138	125-154	$K=6.5232 L^{-0.33741}$	$W=6.5232 \times 10^{-5} L^{3.67256}$
	1930	♂, ♀	433	125-160	$K=4.8834 L^{-0.38067}$	$W=4.8834 \times 10^{-5} L^{3.71033}$
	1931	♂, ♀	338	125-164	$K=38.7640 L^{-0.69345}$	$W=38.7640 \times 10^{-5} L^{3.50755}$
Muskellunge....	1928	♂, ♀	263	145-179	$K=4.568.9 L^{-1.43390}$	$W=4.568.9 \times 10^{-5} L^{1.37710}$
	1930	♂, ♀	244	140-179	$K=567.36 L^{-1.32463}$	$W=567.36 \times 10^{-5} L^{1.76389}$
	1931	♂, ♀	505	130-179	$K=141.92 L^{-0.94953}$	$W=141.924 \times 10^{-5} L^{2.05008}$
Silver.....	1932	♂, ♀	93	145-179	$K=182.87 L^{-0.90613}$	$W=182.87 \times 10^{-5} L^{2.05365}$
	1930-31	♂	110	130-199	$K=0.25532 L^{0.33370}$	$W=0.25532 \times 10^{-5} L^{3.33370}$
	1930-31	♀	160	135-204	$K=0.12322 L^{0.44873}$	$W=0.12322 \times 10^{-5} L^{3.44873}$
Clear.....	1931	♂	85	160-359	$K=0.10104 L^{0.80530}$	$W=0.10104 \times 10^{-5} L^{3.50530}$
	1931	♀	105	170-379	$K=0.04555 L^{0.64991}$	$W=0.04555 \times 10^{-5} L^{3.64991}$
	1932	♂	100	160-379	$K=0.04954 L^{0.82476}$	$W=0.04954 \times 10^{-5} L^{3.82476}$
	1932	♀	85	160-359	$K=0.03652 L^{0.65489}$	$W=0.03652 \times 10^{-5} L^{3.65489}$

¹⁵ For the purpose of fitting the equations the specimens were divided into length groups (10 millimeters in the Clear Lake cisco, 5 millimeters in the other populations) and the average values of K and L determined for each interval. A straight line was fitted to the logarithms of these values by the equating of moments. Combinations of the sexes and of different years' collections were made wherever the data justified the procedure. In Trout Lake and Muskellunge Lake the sexes were combined in each year's collection. In Silver Lake the sexes were treated separately, but the 1930 and 1931 collections were combined. In Clear Lake each sex and each year's collection received separate treatment. The data upon which the equations were based include only the size ranges for which adequate numbers of specimens were available.

TABLE 28.—*Trout Lake ciscoes*.—Values of length, theoretical weight, actual weight, and K at 5-millimeter length intervals

[Sexes combined]

1928				1930				1931			
Length	Calculated weight	Actual weight	K	Length	Calculated weight	Actual weight	K	Length	Calculated weight	Actual weight	K
128.....	29	28	1.33	127.....	25	26	1.22	128.....	28	29	1.38
132.....	31	30	1.31	132.....	27	27	1.18	133.....	31	31	1.32
137.....	33	34	1.31	137.....	31	31	1.17	137.....	33	32	1.25
142.....	37	36	1.28	143.....	34	33	1.14	142.....	36	35	1.24
147.....	40	40	1.27	147.....	36	36	1.15	147.....	39	39	1.21
150.....	43	44	1.28	152.....	40	40	1.13	152.....	42	42	1.21
				157.....	43	43	1.12	156.....	45	45	1.18
				162.....	48	48	1.14	162.....	49	49	1.15
				166.....	51	51	1.11				

TABLE 29.—*Muskellunge Lake ciscoes*.—Values of length, theoretical weight, actual weight, and K at 5-millimeter length intervals

[Sexes combined]

1928				1930				1931				1932			
Length	Calculated weight	Actual weight	K	Length	Calculated weight	Actual weight	K	Length	Calculated weight	Actual weight	K	Length	Calculated weight	Actual weight	K
147.....	44	45	1.40	142.....	36	36	1.24	134.....	33	32	1.34	145.....	38	39	1.24
152.....	46	45	1.28	147.....	38	37	1.18	137.....	34	33	1.28	153.....	46	44	1.27
157.....	48	48	1.25	153.....	41	42	1.16	142.....	37	37	1.30	157.....	47	46	1.22
162.....	51	51	1.21	157.....	43	43	1.11	147.....	40	41	1.28	162.....	50	49	1.18
166.....	52	53	1.16	162.....	45	46	1.08	152.....	42	44	1.26	167.....	52	52	1.12
172.....	55	58	1.13	166.....	47	48	1.04	157.....	45	46	1.19	172.....	55	55	1.08
176.....	57	54	.98	172.....	50	49	.97	162.....	48	49	1.15	176.....	57	58	1.05
				177.....	53	52	.94	166.....	51	49	1.08				
								172.....	55	55	1.09				
								176.....	57	54	.99				

TABLE 30.—*Silver Lake ciscoes*.—Values of length, theoretical weight, actual weight, and K at 5-millimeter length intervals

1930-31, male				1930-31, female			
Length	Calculated weight	Actual weight	K	Length	Calculated weight	Actual weight	K
132.....	29	30	1.28	138.....	30	30	1.15
137.....	32	32	1.24	142.....	34	35	1.19
143.....	37	36	1.23	147.....	38	37	1.16
172.....	69	70	1.36	167.....	68	65	1.19
177.....	76	77	1.37	172.....	65	67	1.32
182.....	83	84	1.39	177.....	72	74	1.32
187.....	91	91	1.39	182.....	79	81	1.33
191.....	98	99	1.42	187.....	87	89	1.34
197.....	108	106	1.38	192.....	95	95	1.35
				196.....	102	102	1.34
				201.....	111	108	1.33

TABLE 31.—*Clear Lake ciscoes*—Values of length, theoretical weight, actual weight, and *K* at 10-millimeter length intervals

1931, male				1931, female				1932, male				1932, female			
Length	Calculated weight	Actual weight	K	Length	Calculated weight	Actual weight	K	Length	Calculated weight	Actual weight	K	Length	Calculated weight	Actual weight	K
167	62	68	1.47	177	73	76	1.38	168	57	59	1.26	155	42	43	1.13
174	72	70	1.37	183	83	85	1.36	176	69	68	1.24	175	68	68	1.26
182	84	80	1.34	197	108	106	1.39	183	79	79	1.29	180	76	75	1.29
203	124	124	1.48	201	116	122	1.51	215	141	138	1.39	195	106	100	1.43
204	204	195	1.53	231	193	184	1.49	234	192	182	1.42	255	268	268	1.62
246	241	240	1.62	244	237	226	1.54	245	227	226	1.53	265	314	309	1.69
253	268	272	1.67	256	280	284	1.69	255	262	244	1.47	274	338	351	1.64
265	316	316	1.70	266	321	312	1.68	264	297	292	1.53	290	394	433	1.62
273	351	330	1.62	275	365	352	1.69	273	335	370	1.82	306	520	529	1.81
282	392	385	1.71	283	406	385	1.69	288	407	434	1.75	315	594	588	1.90
293	448	445	1.77	296	480	462	1.77	294	437	443	1.85	324	695	650	2.05
301	493	465	1.71	303	522	546	1.96	302	484	508	1.80	334	704	724	1.90
316	582	595	1.89	314	589	570	1.84	315	565	563	1.90	345	812	821	1.98
322	624	663	1.99	327	686	712	2.05	326	634	657	1.90	356	984	923	2.18
333	700	708	1.92	335	752	766	2.04	334	695	708	1.91	365	1,002	1,012	2.06
343	777	803	2.00	345	833	866	2.07	343	767	773	1.92	373	1,107	1,091	2.12
350	834	850	1.98	353	905	933	2.12	352	847	840	1.82	384	1,198	1,212	2.12
				362	997	1,036	2.18	365	960	885	1.79				
				371	1,088	1,048	2.05								

The comparisons of theoretical and actual weights show that the equations of table 27 fit the observed data in a quite satisfactory manner, for in general the agreement between actual and calculated weights is good. The discrepancies between actual and calculated weights are greater in the Clear Lake samples (table 31) than in those of the other three lakes. This might be expected not only because of the smaller numbers of fish in the Clear Lake collections but also because of the much greater size range shown by the ciscoes of this lake.

The equations themselves (table 27) contribute interesting information relative to the problem discussed previously (pp. 238–242) concerning the use of *C* as a coefficient of condition. The examination of the values taken by $C \times 10^6$ shows how widely this quantity can vary not only within different populations of the same species but also in different sexes and in different years' collections of the same population. Certainly the value 0.03652 (Clear Lake females, 1932) cannot be compared directly as a measure of condition with the value 4,568.9 (Muskellunge Lake, 1928), particularly in view of the fact that the higher value of *C* pertains to the slenderer form. Nor can the higher values of *C* shown by the males in the Clear Lake equations be interpreted as showing the males of this population to be in better condition than the females. The actual values of *K* and of weight for length show that the reverse is true. The table shows yet other examples that demonstrate clearly that values of *C* cannot be compared either between the sexes or between different years' collections of the same population, much less between different populations.

If the variations in the value of *C* are examined in relation to variations in the values of the exponents, *m* and *n*, it may be seen again that the values taken by *C* depend on the values taken by *n*. If *n* is high, *C* is small—and the reverse. Thus it may be seen that here as in Järvi's data the values of *C* do not depend on relative heaviness but on the rate of change in relative heaviness as measured by the exponents, *m* and *n*.

The examination of the values taken by *n* show further that this quantity is not fixed either for a species or a population. The values of the exponent not only vary tremendously from lake to lake but also vary considerably from year to year in the

samples of a single population. It will now be shown that not only does n vary from population to population and from year to year in the same population but further that in two populations, at least, the values of n determined for a single year's sample apply only to the length intervals for which the equations were fitted and do not hold for fish whose lengths lie outside these length ranges.

If the equation, $K=C \times 10^5 L^m$, for each year's collection of the Muskellunge Lake cisco is solved for $L=100$ millimeters the following values of K are obtained: 1928, $K=2.59$; 1930, $K=1.93$; 1931, $K=1.80$; 1932, $K=1.86$. These values of the coefficient of condition indicate a fairly robust body form. Ciscoes of such heavy build are indeed found among the larger fish of the Clear Lake population (table 31), but it is very unlikely that such heavily built individuals may be found at the length of 100 millimeters in the Muskellunge Lake cisco population, or in any population of the same species. This view is supported by the comparison of the K values upon which the 1928 length-weight relationship was determined (table 29) with those of the 15 fish that were less than 145 millimeters long. Eight of these 15 fell in the 125–129 millimeter length interval and had an average value of 1.23 for the coefficient of condition, K ; the 5 individuals in the 130–134 millimeter interval had an average K value of 1.25; while 2 single individuals whose lengths were 138 and 144 millimeters had K values of 1.29 and 1.34, respectively. These data show that in 1928 the values of K in Muskellunge Lake ciscoes less than 145 millimeters long were much lower than the theoretical length-weight equation (based on specimens more than 145 millimeters long) indicated they should be.

The 1931 data for Trout Lake furnish another example of the failure of a length-weight equation to describe the length-weight relationship for fish outside the length range for which the equation was determined. The length-weight equation for 1931 (see table 27) was based on specimens whose lengths ranged from 125 to 164 millimeters. The same collections contained five large fish (189 to 225 millimeters long). Since the 1931 length-weight equation for Trout Lake indicates a continuous decrease of K with increase in length, these large fish would be expected to show small values for the coefficient of condition. Table 32 which contains a comparison of actual and theoretical values of weight and K for these five fish shows that they fail completely to fulfill this expectation, for the actual values of weight and K are far above the theoretical values calculated from the length-weight equation.

TABLE 32.—Values of length, weight, and K for the 5 longest individuals of the 1931 Trout Lake cisco collection

Age	Length	Calculated weight	Actual weight	Calculated value of K	Actual value of K
VIII.....	189	69	100	1.03	1.48
XI.....	192	73	90	1.02	1.27
VIII.....	203	82	122	.98	1.46
XI.....	218	97	148	.93	1.43
XII.....	226	105	172	.91	1.49

Observations on the failure of a single value of n to hold for all lengths of fish within a population have been made previously by Clark (1928), Walford (1932), and Schultz (1933).

Materials for the comparison of condition in the different populations and in different years are to be found in tables 28 to 31 and 33. The last-named table

shows the variation in K according to age, while the earlier tables show the variation of K with length. On the whole the changes of K with age depend on differences in the average length of the various age groups. In Clear Lake in particular large differences in average lengths of age groups are associated with large differences in the average value of K , while smaller differences in average length are associated with smaller differences in the average value of K .

TABLE 33.—*Value of K according to age groups*

[Number of specimens in parentheses]

Age	Trout Lake			Muskellunge Lake			Silver Lake		
	1928	1930	1931	1928	1930	1931	1928	1930	
								Male	Female
XII			1.49 (1)						
XI			1.35 (2)						
X									
IX									
VIII			1.47 (2)						
VII									
VI			1.14 (2)						1.39 (3)
V		1.17 (9)	1.18 (23)				1.34 (10)	1.38 (10)	1.37 (15)
IV	1.32 (17)	1.15 (99)	1.21 (139)			1.10 (2)	1.29 (69)	1.42 (23)	1.37 (35)
III	1.28 (61)	1.13 (347)	1.24 (129)	1.11 (10)	1.06 (14)	1.13 (266)	1.30 (46)	1.38 (13)	1.34 (12)
II	1.30 (102)	1.16 (36)	1.30 (50)	1.23 (252)	1.07 (214)	1.28 (229)	1.29 (9)	1.28 (3)	1.25 (4)
I	1.24 (2)		1.28 (2)	1.24 (19)	1.18 (17)	1.28 (9)	1.19 (1)		

Age	Silver Lake, 1931		Clear Lake			
	Male		1931		1932	
			Male	Female	Male	Female
XII						
XI						2.20 (1)
X					2.15 (1)	2.00 (1)
IX					2.12 (1)	2.36 (2)
VIII						
VII			1.97 (3)	2.13 (11)	1.99 (7)	2.16 (8)
VI			2.00 (6)	2.12 (17)	1.95 (9)	2.09 (12)
V		1.36 (8)	1.96 (7)	2.06 (8)	1.82 (2)	2.50 (1)
IV	1.40 (12)	1.34 (22)	1.88 (2)	2.10 (1)	1.93 (7)	1.93 (7)
III	1.41 (13)	1.28 (22)	1.86 (5)	2.03 (7)	1.83 (11)	1.90 (14)
II	1.31 (10)	1.29 (13)	1.73 (17)	1.86 (19)	1.70 (23)	1.82 (21)
I	1.30 (4)	1.25 (8)	1.66 (28)	1.66 (27)	1.56 (20)	1.64 (13)
	1.22 (24)	1.18 (25)	1.38 (18)	1.39 (15)	1.25 (20)	1.27 (11)

The analysis of the data was made to include the examination of variation of K with size in fish of the same age and the variation of K with age in fish of the same size. Without presentation of the extensive tabular material that would be necessary to show the detailed results of these analyses it may be stated that the variation of K with length within an age group proceeds in the same direction as the variation of K with length in the population as a whole, and that, on the whole, the value of K appears to be independent of age in fish of the same length.

The tables 28, 29, 30, 31, and 33 show further that condition varies from year to year in the same population. In both Trout Lake and Muskellunge Lake the ciscoes were slenderer in 1930 than in 1928 or 1931. In Silver Lake the lack of sex records for 1928 makes a comparison of that year with later years difficult. There is some indication, however, that in 1928 the Silver Lake cisco may have been in poorer condition than in 1930. In Clear Lake there do not appear to be any notable differences in the condition of the cisco in 1931 and 1932.

With respect to average condition, from poorest to best, the populations fall in the following order: Muskellunge Lake (sexes combined), Trout Lake (sexes combined), Silver Lake females, Silver Lake males, Clear Lake males, and Clear Lake females.

The order of the four populations of this investigation with respect to average condition is the same as their order with respect to average duration of life (p. 267). The indicated association between condition and longevity finds support in the observation (table 32, p. 246) that in Trout Lake survival to an advanced age appears to be accompanied by, if not contingent upon, a departure from the general tendency for condition to become poorer with increased length.

The study of condition and of the length-weight relationship in these four cisco populations may well be concluded with an illustration of how progressive change of condition is reflected in a progressive change in body proportions. In order to determine the intensity of the excess vertical and lateral growth that produced the heavy body form in the older and larger Clear Lake ciscoes the relationship of length to depth and width was studied in 95 preserved specimens collected in 1932. Since the relationship of length to weight in the Clear Lake cisco can be expressed satisfactorily by a parabolic equation it was assumed that a similar relationship may hold between length and width and length and depth. On the basis of this assumption the following equations were derived:

Male—46 specimens:

$$\text{Depth} = 5.052 \times 10^{-2} L^{1.2939}$$

$$\text{Width} = 0.656 \times 10^{-2} L^{1.5502}$$

Female—49 specimens:

$$\text{Depth} = 5.230 \times 10^{-2} L^{1.2899}$$

$$\text{Width} = 0.173 \times 10^{-2} L^{1.7879}$$

L = length in millimeters.

TABLE 34.—*Clear Lake ciscoes, 1932—Comparison of theoretical and actual values of body depth and body width*

Males					Females				
Length	Calculated depth	Actual depth	Calculated width	Actual width	Length	Calculated depth	Actual depth	Calculated width	Actual width
165.....	37	36	18	19	150.....	34	34	13	13
175.....	40	38	20	19	165.....	38	37	16	20
181.....	42	44	21	21	172.....	40	40	17	19
206.....	50	49	25	26	190.....	46	48	20	24
235.....	59	62	31	31	265.....	69	68	37	36
255.....	66	68	35	35	274.....	73	72	39	35
266.....	69	69	37	36	295.....	80	80	45	41
284.....	76	79	42	41	305.....	84	85	48	47
292.....	78	81	44	43	314.....	87	87	50	49
302.....	82	81	46	47	324.....	90	86	53	45
316.....	86	87	49	43	334.....	94	92	56	54
325.....	90	89	51	51	345.....	98	99	59	64
334.....	93	91	54	56	355.....	102	105	63	67
345.....	97	92	56	63	362.....	105	111	65	69
					376.....	110	111	69	65
					383.....	113	109	72	59

Table 34 shows the lengths, depths, and widths from which the above equations were calculated. The data of the same table also make possible the comparison of actual measured depths and widths with theoretical values calculated from the equations. If due consideration is given the small number of specimens the agreement between the actual and theoretical values of depth and width is, in general, good.

The equations show that both the males and females of the Clear Lake cisco grow more rapidly in depth and width than in length. The differential growth of the dimension, width, proceeds more rapidly than the differential growth of the dimension, depth, that is, the change to a heavier stature proceeds more rapidly along the lateral than along the vertical axis. The comparison of the equations for the two sexes shows further that the differential growth in depth proceeds at approximately the same rate in the males and the females, while the differential growth in width proceeds more rapidly in the females than in the males. It is this higher differential growth in width that accounts for the higher K values in the Clear Lake females.

Values of K for cisco populations have been presented by Van Oosten (1929) and by Hile (1931). The former author found K to have an average value of 1.13 for the Lake Huron herring (0.01126 in his method of presentation). The sexes showed no consistent differences, and there was only a slight tendency for the value of K to increase with increase in length. Hile's data on the cisco of the Indian Village Lakes (Indiana) were too scanty to afford any information on the change in the value of K with change in length. The largest value of K which he found for any age group was 1.79, the smallest, 1.56. Since both Van Oosten and Hile employed the cube relationship for the calculation of K values, their results can be compared directly with those of this study.

A comparison of the values of K in the Lake Huron herring and the Indian Village Lakes cisco with those of the populations of this study shows that the Lake Huron herring is a very slender fish of approximately the same relative heaviness as the Muskellunge Lake cisco, while the Indian Village Lakes cisco is more heavily built than the Trout Lake, Muskellunge Lake, and Silver Lake ciscoes, but sligher in form than the Clear Lake cisco.

LENGTH OF GROWING SEASON

It was not possible in this investigation to follow the course of the season's growth in the different populations by means of a systematic collection of specimens at different times throughout the spring, summer, and autumn. Since all collections were made in July, August, and early September, and the single year's collections within a single lake were frequently made within a period of only a few days, any estimate of the course of growth during the growing season or of the length of the growing season in the different lakes must depend largely upon an indirect approach. However, the fact that the growth materials from each lake represent collections in 2 or more years makes possible at least a rough estimate of the length of the growing season in each lake. The following example will illustrate the method by which these estimates may be made:

The 1928 collection of the Trout Lake cisco contained 102 specimens of the II group (1926 year class). These fish had an average length of 134 millimeters at the time of capture (July 21, 28, and 29). The calculation of their earlier growth from scale measurements indicated that their average length at the beginning of the 1928 growing season (end of second year of life) was 117 millimeters. Thus it may be seen that these II-group fish of 1928 had grown 17 millimeters between the beginning of the growing season and the time of their capture in late July. The question now arises as to what part of the total 1928 growth of the II group this 17-millimeter increment may represent. The presence of this same (1926) year class in the 1930 collections as the IV group and in the 1931 collections as the V group makes a quite reliable answer to this question available, for it is possible to calculate the total

1928 growth from the scale measurements of each of these later collections of the year class. The 1930 IV-group samples indicated that the 1926 year class had a total growth of 19 millimeters in 1928, while the 1931 V group gave an average calculated growth of 17 millimeters for the same year. The combination of the 1930 and 1931 data gives a calculated total growth of 18 millimeters for the 1926 year class in the calendar year 1928. Since the 1928 specimens themselves had grown 17 millimeters at the time of their capture in late July it is apparent that the 1928 II group had practically completed its season's growth at the time of capture of the samples.

It is obvious that comparisons of the sort given above, to be most dependable, should be based on different years' collections of the same year class. By such a procedure errors that might arise from unequal growth of the same age fish in different calendar years are completely avoided. The confining of comparisons to different years' collections of the same year class of course limits this type of analysis to those year classes that are well represented in more than 1 year's collection. However, for the question at hand dependability is more important than a diversity of material.

Since data of the above type throw light only on the probable time at which growth ends, the presentation of the available data on the amount of the season's growth already made by the different populations at the time of capture of the samples should be preceded by a brief consideration of probable time at which the season's growth begins. Juday and Birge (1930) stated that in the lakes of this region "The ice disappears about the 1st of May; the shallower lakes usually lose their covering of ice a few days before the larger and deeper lakes." From these facts it may be considered valid to assume that in general growth does not occur in any of the four populations of this study before early May, and that the time at which growth begins does not differ by more than 1 or 2 weeks from one lake to another.

Table 35 shows a comparison of the amount of calculated growth made by three age groups of the Trout Lake cisco between the beginning of the growing season and the time of capture of the samples, with the total calculated growth for the season as determined from later years, collections of the same year class. The data for the 1928 II group which were used to illustrate the method of comparison have already been discussed. It may be seen at once that the 1930 III and IV groups agree with the 1928 II group in indicating that the season's growth of the Trout Lake cisco is practically if not entirely complete by the end of July. The growing season for the Trout Lake cisco is not longer than 3 months and, since growth may not start at once upon the disappearance of the ice, may actually be somewhat less than 3 months.

TABLE 35.—*Calculated growth of 3 age groups of the Trout Lake cisco up to the time of capture in the summer, compared with the growth for the entire summer calculated from collections of the same year class in later years*

[Number of specimens in parentheses]

Year class	Date of capture	Age at time of capture	Growth in summer up to time of capture	Growth in entire summer based on later collections of	
				1930	1931
1926	July 21, 28, 29, 1928.....	II	17 (102)	19 (99)	17 (79)
1926	July 29, 30, 31, 1930.....	IV	9 (99)	-----	9 (79)
1927	Do.....	III	10 (347)	-----	11 (269)

Only one year class (1928) occurred in sufficient numbers in more than 1 year's collection of the Muskellunge Lake cisco to make possible a comparison of growth up to time of capture with the total season's growth. The 1930 II group (see table 4) had an average calculated growth of 19 millimeters for the 1930 season up to the time of capture, August 28 and 29. The 337 specimens of this same year class taken as the III group of 1931 showed an average calculated growth of 18 millimeters for the entire 1930 season. Although these data can scarcely be taken to demonstrate a shrinkage of 1 millimeter in the average size of the 1930 II group between the time of capture of the samples and the time of the formation of the third annulus, they do indicate that the season's growth of the Muskellunge Lake cisco is complete at the end of August.

It is, of course, possible that growth in the Muskellunge Lake cisco may be complete several weeks before the end of August. The 1928 and 1931 collections were taken earlier in the summer but, unfortunately, no comparisons are possible between the data of any age groups of the samples of these 2 years and data based on collections of the same year class in other years. In the 1928 collections (made July 1 to July 4) only the II group was well represented and none of the 1926 year class individuals was taken in any of the later collections. The 1931 collections (made July 14 to 28—over 80 percent of the former date alone) cannot be compared with the 1932 collections since for reasons discussed previously (p. 219) the 1932 catches were not included in the Muskellunge Lake growth data. It is possible, however, to compare the season's growth before capture of the 1928 and 1931 II groups with the grand average of 18 millimeters calculated growth in the third year of life, based on the combination of all age groups above the II group and all years' collection. These comparisons show that the 1928 II group which had grown 13 millimeters at the time of capture in early July was still 5 millimeters short of the average growth of fish in the third year of life, while the 1931 II-group fish which had grown 11 millimeters up to the middle of July still lacked 7 millimeters of having attained the average for third-year growth. These two comparisons, particularly the latter, indicate that the Muskellunge cisco is growing actively throughout July and that in all probability this growth extends at least into early August. Consequently the Muskellunge Lake cisco may be accredited with a slightly longer growing season than the Trout Lake cisco.

Since it was felt that the prominence of Lee's phenomenon in the growth data of the Silver Lake cisco made the comparison of age groups separated by more than 1 year of life inadvisable, none of the 1928 material was used in the study of length of the growing season in that lake. Table 36 shows the comparison of the 1930 calculated growth of three age groups of the Silver Lake cisco up to the time of capture in the middle of August with the total 1930 growth of these age groups calculated from 1931 collections of the same year classes. It may be seen that at the time of capture of the 1930 samples, August 9 to 15, the season's growth of the Silver Lake cisco was approximately two-thirds to three-quarters complete. From this fact it may be concluded that the Silver Lake cisco is still growing throughout the month of August and that the growing season probably extends on into early September. It may be concluded, therefore, that the growing season of the Silver Lake cisco is longer than that of either the Trout Lake or the Muskellunge Lake cisco.

TABLE 36.—*Calculated growth of 3 age groups of the 1930 Silver Lake cisco collections up to the time of capture in the summer, compared with the growth for the entire summer of 1930 calculated from collections of the same year classes in 1931*

[Number of specimens in parentheses]

Year class	Date of capture	Age at time of capture	Growth in summer up to time of capture	Growth in entire summer based on 1931 collections
1925	Aug. 9, 10, 15, 1930.....	V	8 (25)	12 (21)
1926	Do.....	IV	10 (58)	14 (108)
1927	Do.....	III	14 (25)	17 (102)

The 1931 Clear Lake cisco samples were collected in two groups, the first from July 22 to 28, and the second from September 2 to 5. Tables 37 and 38 show the calculated growth during 1931 up to these 2 periods of capture for 7 age groups (sexes considered separately) and also the entire 1931 growth for these age groups as calculated from 1932 collections of the same year classes. Although there are several irregularities in the tables it can be seen at once that much of the season's growth occurred after the latter part of July and that growth was by no means entirely completed in early September. If all age groups are considered together, the males taken in late July had completed 64 percent of their 1931 growth while those taken in early September had completed 81 percent of the season's growth; the same data for the females are 68 percent for the July samples and 76 percent for the September samples. From these facts it may be concluded that the growth of the Clear Lake cisco probably continues through September and possibly into October, and further that the growing season of the Clear Lake cisco is longer than in any of the other three lakes.

TABLE 37.—*Calculated growth of 7 age groups of the Clear Lake cisco (males) up to the time of capture in the summer of 1931, compared with the entire 1931 growth calculated from the same year classes in the 1932 collections*

[Number of specimens in parentheses]

Year class	Age at time of capture in 1931	1931 growth up to July 22-28	1931 growth up to Sept. 2-5	Total 1931 growth based on 1932 collections	Year class	Age at time of capture in 1931	1931 growth up to July 22-28	1931 growth up to Sept. 2-5	Total 1931 growth based on 1932 collections
1924.....	VII	8 (7)	5 (1)	11 (7)	1928.....	III	27 (16)	33 (10)	42 (11)
1925.....	VI	9 (6)	10 (5)	13 (9)	1929.....	II	51 (27)	61 (7)	70 (23)
1926.....	V	13 (2)	14 (2)	16 (2)	1930.....	I	55 (16)	77 (4)	105 (20)
1927.....	IV	18 (6)	22 (4)	24 (7)					

TABLE 38.—*Calculated growth of 7 age groups of the Clear Lake cisco (females) up to the time of capture in the summer of 1931, compared with the entire 1931 growth calculated from the same year classes in the 1932 collections*

[Number of specimens in parentheses]

Year class	Age at time of capture in 1931	1931 growth up to July 22-28	1931 growth up to Sept. 2-5	Total 1931 growth based on 1932 collections	Year class	Age at time of capture in 1931	1931 growth up to July 22-28	1931 growth up to Sept. 2-5	Total 1931 growth based on 1932 collections
1924.....	VII	9 (16)	7 (5)	12 (8)	1928.....	III	31 (18)	36 (7)	44 (14)
1925.....	VI	12 (6)	12 (6)	18 (12)	1929.....	II	55 (27)	60 (8)	77 (21)
1926.....	V	12 (1)	13 (1)	16 (1)	1930.....	I	63 (14)	78 (4)	105 (13)
1927.....	IV	26 (2)	26 (2)	32 (7)					

While the Clear Lake cisco undoubtedly has an advantage over the other three populations in the length of the growing season, this advantage may not be as great as might at first be suspected. The autumn of 1931, in which year the length of the growing season of the Clear Lake cisco was estimated, was abnormally warm. The records¹⁶ of the United States Weather Bureau station at Minocqua, about 6 kilometers west of Clear Lake, show that the air temperature in September 1931, was 4.5° F. above the normal, while in October and November it was 3.0° F. and 6.5° F. above normal, respectively. This warm autumn may have extended the growing season of the Clear Lake cisco beyond its normal limit. If this is true the growth beyond early September in normal years may not be as much as 20 percent or more of the season's growth as tables 37 and 38 would indicate.

If the length of the growing season in the different lakes is considered in relation to the growth rates of the various populations, it may be seen that poorest growth occurs in the lake with the shortest growing season (Trout Lake) while the best growth occurs in the lake with the longest growing season (Clear Lake). The two lakes (Muskellunge and Silver Lakes) in which the growth rate was intermediate also have growing seasons of intermediate length. Thus it appears that differences in the length of the growing season are important contributing factors toward differences in growth rates. However, these differences in the length of the growing season can by no means explain entirely the observed differences in the amount of growth in the four populations. The growth of the Clear Lake cisco up to July, for example (tables 37 and 38), is well in excess of that found in Trout Lake cisco (table 35) or the Silver Lake cisco (table 36) of corresponding ages at any time in the growing season or for the entire growing season.

RELATIONSHIP BETWEEN DENSITY OF POPULATION AND RATE OF GROWTH

It was stated in the introduction that these studies on the growth of the cisco have been made on populations from "type" lakes that were selected on the basis of their biologically productive capacities as estimated chiefly from the amounts of fixed carbon dioxide in their waters. It was hoped that the comparison of the growth of the various populations might yield information as to the extent and nature of the effect of the natural richness of the waters upon the growth rates of the fish populations that live in them. The investigators who collaborated in planning and initiating the studies of which the present one is a part harbored no delusions to the effect that the relationship between the growth of fishes and the environment is in any sense simple. It was nevertheless surprising to find early in the investigation of the growth of the cisco that the growth rates of the populations did not fall at all in the order of the estimated productive capacities of the lakes in which they occurred, but rather that the reverse was true. Trout Lake with 18.7 parts per million of fixed CO₂ contains the slowest growing cisco of the four populations, while the cisco of Clear Lake, in which body there occur only 2.2 parts per million of fixed CO₂, stands out by far as the fastest growing of the four stocks. In Silver Lake and Muskellunge Lake where the amounts of fixed CO₂ are intermediate in value (Silver, 15.5 parts per million; Muskellunge, 10.0 parts per million) the growths of the cisco populations are also intermediate.

It can hardly be concluded that an inverse causal relationship exists between the growth rate of the cisco and the fixed CO₂ content of the lake it inhabits. Rather

¹⁶ Climatological Data of the United States by Sections, vol. 18, 1931.

it would appear that the growth rate of the cisco in these lakes depends primarily on some factor other than that of the productive capacity of the lake as that capacity is estimated from the concentration of bound CO_2 in its waters. If it is assumed that the various stocks do not differ greatly in their hereditary capacities for growth and that environmental conditions are in general comparable, then it may be expected that the amount of growth in the various populations will depend in large measure upon the availability of food. The determining factor is then the amount of food available to each individual fish. If the poorest growth occurs in the lake that produces the greatest amount of food, it may be assumed that here in all probability the number of feeding individuals is so great and the competition for food so strong that these individuals cannot secure a sufficient amount of food to maintain their normal rate of growth. On the other hand, if a relatively rapid growth occurs in a lake with a scanty basic supply of food it may be assumed that the feeding population in that lake is so small that in spite of the scarcity of food the individuals are still able to secure sufficient nourishment to maintain rapid growth.

This conception of a dependence of growth upon density of population is based primarily upon the assumption that there exists a competition for food. If food is present in a quantity greater than the maximum which the population can utilize for purposes of maintenance and growth, then an increase in the density of the population should not affect its growth rate until that point is passed where the food available becomes less than the maximum quantity which the population can use. From this point on a continued increase in the density of population involves a decrease in the ration of the individual fish and reduces the amount of individual growth. If the density of the population becomes sufficiently great, there is finally reached the point at which the food supply suffices only for purposes of maintenance and there is no excess for growth.

The evidence that investigators have presented to show a relationship between density of population and rate of growth in fishes has been of two sorts: (1) Change in rate of growth accompanying transfer from a thickly populated to a sparsely populated region, and (2) change in rate of growth accompanying changes in the density of the population within the same region.

European investigators have conducted numerous experiments that show the effect on growth rate of transplanting young plaice from the overcrowded coastal nursery grounds to less densely populated areas with more abundant food. The classic of all such experiments is the Danish work of transplanting young plaice from the overcrowded nursery grounds at the entrance of the Limfjord to the thinly populated areas of the inner broads. Although three-fourths of the fish are retaken within the year following the time of their liberation, their increase in size is so great that a continuation of these transplantation operations, which were begun in 1892, has proved profitable up to the present time.¹⁷

Borley (1912) gave the results of experimental transplantation of plaice from the English coastal waters to the Dogger Bank. He believed that there was "at least a doubling of the growth" (in length). In the same paper Borley reviewed the results of similar experiments by Dutch and Danish investigators. Lee and Atkinson (1912) also reviewed the results of earlier transplantation experiments. A good general review of European plaice transplantation experiments may be found in Blegvad's paper published in 1933.

¹⁷ There was no transplantation in 1917. Johansen (1928) summarized the results of the transplantation operations in the Limfjord up to that time.

The study of the relationship between the density of population in marine fishes and their rate of growth received considerable stimulation from the observation of the conditions that resulted from the almost complete suspension of fishing operations in the North Sea during the World War. During the war there occurred an accumulation of the stock of plaice. Large fish became more plentiful but the average rate of growth decreased. With the resumption of fishing on a large scale the accumulated population was largely fished out. Large fish became relatively scarce and the average rate of growth increased. Further investigations disclosed the fact that in general in regions with a dense population of plaice the rate of growth tended to be low and vice versa.¹⁸

Bückmann (1932) expressed the relationship between growth in weight and the density of population as being inversely proportional and referred to it as a "Vereinfachtes Wachstumsgesetz" which he defined: "Die Gewichtszunahme verhält sich umgekehrt proportional zur Bestandsdichte." Bückmann expressed this law by the equation,

$$w^1 = w \frac{n}{n^1},$$

where w is the weight increase per individual in a population of n individuals and w^1 is the increase in weight that would occur if the number of individuals were changed from n to n^1 . Bückmann recognized the law to be inexact and mentioned certain disturbing influences. He pointed out that it is incorrect to assume that all the food consumed is applied toward increase in size. A certain definite amount is utilized to maintain individual metabolism. The percentage of the food that is so used varies according to the total amount of food available to each individual. Further, the efficiency with which a fish makes use of its food varies according to the abundance of food at hand.¹⁹ Yet another complicating factor is the competitive action of other species. Bückmann developed a growth formula that contained correcting factors for these sources of error.

Russell (1932) made a somewhat similar analysis of the relationship between growth and population density in fishes.

In some species fluctuations in the density of the population appear to have no effect on the rate of growth. Concerning the haddock Bowman (1932) stated:

It cannot be inferred from the results of the extensive and continuous investigations that, in comparable areas, the average growth rates of successive broods in their first year of life vary with differences in brood densities.

Hjort (1932) pointed out that growth in the Norwegian cod and herring stocks is remarkably uniform from year to year and quite independent of the density of the stock. He contended that growth was determined by specific conditions in the sea rather than by the numbers of fish in the population.

Marine populations, particularly round fishes, can wander freely over extensive areas. It is possible for them to seek out those regions with the most suitable food conditions, and in some instances it is probable that the role of food as a limiting factor for growth is insignificant as compared to other environmental influences. Within the restricted limits of a small inland lake a closer dependence of the growth

¹⁸ The following papers listed in the bibliography touch upon the question of the relationship between density of population in marine fishes (largely the plaice) and their rates of growth: Strodttmann and Langhammer (1925), Heincke and Bückmann (1926), Garstang (1926), Jensen (1928) and (1932), Bückmann (1932), Bowman (1932), Hjort (1932), and Russell (1932). These papers are only representative of the rather voluminous literature of the subject.

¹⁹ Bückmann referred to Dawes' (1930, 1931) feeding experiments with plaice.

rate upon the density of the population might be expected. Here ordinarily it is impossible for underfed fish to move to an area with more abundant food; they must subsist as best they can upon the food supply available within the lake. If the lake contains a "natural" population, a population not disturbed by any extensive removal of individuals through a fishery, then it may be assumed that in all probability a competition for food exists, and that this competition may in some lakes be quite severe. Several examples of the dependence of fish growth upon the density of the population have been observed in fresh-water lakes.

The Norwegian farmers have long recognized the disadvantages of an overcrowded stock in trout lakes. The appearance of emaciated and undersized individuals is taken as an indication that a more intensive fishery is desirable. Through the regulation of the intensity of the fishery they "keep the trout under discipline" (Huitfeldt-Kaas reviewed by Rugde (1923) in the *Salmon and Trout Magazine*). In another paper Huitfeldt-Kaas (1927) stated, "Very great rapidity of growth is shown by fish [trout] in lakes with quite small stock * * * This type of growth I think can suitably be termed '*slender stock type*'."

Surbeck (1921) stated that the decrease in numbers in the stock of the "Balchen" (*Coregonus schintzii helveticus* Fatio) in Vierwaldstättersee following 1900 was accompanied by a significant increase in individual size.

Järvi (1920 and 1924) was able to show that in the "kleine Maräne" (*Coregonus albula*) of the Finnish lakes the poorest growth occurred when the fish were most plentiful and the best growth occurred when the fish were scarce. The fishermen consider the presence of large young fish in the early catches of the fishing season as an indication that the year will be bad.

Pirognikoff (1927) stated that the decline of the intensity of the fishery for the rudd (*Rutilus rutilus lacustris* Pallas) in Lake Chani and the consequent increase in the abundance of that form was accompanied by a distinct decline in the rate of growth.

Hart (1931) found that whitefish taken in different parts of Lake Ontario showed different rates of growth, which he was able to explain in part by the selective action of the gear used in collecting the samples, but stated with reference to the slow growth of the fish taken at Pleasant Point, "An explanation on the grounds of detrimentally keen competition for food in the first years in the neighborhood of a much frequented spawning ground is a tempting one."

In his studies of the trout (*Salmo kamloops* Jordan) of the Kamloops district, British Columbia, Mottley (1932) observed that the opening of a lake to intensive fishing was followed not only by a decrease in the abundance of trout but also by an increase in their "size for age." He advocated that an annual determination of growth rates be included in the data upon which stocking policies for the lakes of the region are based.

Juday and Schneberger (1933) reported the discovery of abundant populations of undersized smallmouth black bass in two small lakes in Vilas County, Wis. They considered the inferior growth of these bass as the results of a too great density of the populations in relation to the amount of available food.

On the basis of experimental studies on young trout Willer (1929) asserted that crowding operates as an inhibitor to growth in a manner over and above the effect it may have in producing competition for food. He considered this "Raumfaktor" to account for the irregularities found by him (Willer, 1924), and by Järvi (1920) in

the growth of the kleine Maräne and stated that he had found the same situation in the smelt (Willer, 1926).

In view of the numerous demonstrations by other investigators of a relationship between density of population and growth rate in fishes it was considered advisable in this study to investigate the relative densities of the four cisco populations with particular reference to a possible relationship between these densities and the observed differences in the growth rates of the various stocks.²⁰

An important source of difficulty in the study of the relationship between population density and growth rate lies in the fact that the estimation of the density of a fish population, either absolute or relative, is at its best difficult and in a large measure uncertain. Ordinarily the chief sources of information are the results of experimental fishing and the statistics of the commercial yield. In the present investigation dependence must be placed entirely upon the size of the catch per unit of effort as based on the action of experimental gear (gill nets). In this connection some of the chief difficulties and sources of error in the gathering and the interpretation of data on the gill-net catches should be mentioned.

Gill nets fish from a fixed position, and their effectiveness is dependent upon the movements of the fish. If the amount of movement varies according to time, locality, or population, such variations will be reflected in the catch of the net. The effect of the movements of the cisco is complicated by a tendency for the fish to shoal or move in groups. Group movements cause a great variation in the catch from day to day from nets set in exactly the same location.

Further difficulty lies in the fact that the catches of the same net or the same group of nets in different lakes are not always directly comparable.²¹ For example, the seven mesh sizes of the "new" gear employed in collecting the samples for the later part of this investigation failed to take equally adequate samples of all the age groups in the different populations. The Clear Lake catches probably represent reliable samples of the I group and all older groups as well. In Silver Lake and Muskellunge Lake, however, the I groups cannot be considered adequately represented, while in Trout Lake the representation of the II group as well as the I group are to be considered too small. The comparison of the Clear Lake catches with those in which the I and II groups are absent or poorly represented would of course lead to a too high estimate of the relative density of the Clear Lake population.

It must be recognized also that the fishing effort represented by a series of nets varies from one lake to another, for obviously no effort can be accredited to a net that is wholly ineffective for the capture of the members of a particular population. On the other hand, in a population with a wide length range two or three sizes of mesh may be necessary to capture a sample directly comparable to the catch of a single mesh size in a population with a more compact size range. Because of these difficulties it is not possible on the basis of gill-net catches to derive "index numbers" that can be taken directly as reliable measures of relative densities in populations of greatly dissimilar size ranges. In general, however, the examination of the catch of each size of mesh in each lake will, in spite of these aforementioned difficulties, give a fairly good idea of relative population densities in different lakes.

²⁰ It is realized that competition for food is not at all confined to competition among individuals of the same species. With the possible exception of the Muskellunge Lake cisco population, however, the competition of other species is probably of insignificant importance in this study. At present there are available few data on the degree of competition between the Muskellunge Lake cisco and the perch that occur abundantly in the same regions of the lake. (See the section, Fishes Associated with the Cisco.)

²¹ For a more detailed discussion of the action of gill nets see the section, "The selective action of gill nets."

In the comparison of net catches from different lakes it is important further to know whether observed differences in net catches result from real differences in population densities or whether they depend merely upon the actual positions in which the nets were set within the lakes. For this purpose it is necessary to have some knowledge of the vertical distribution of the cisco in each of the lakes whose populations are to be compared. The importance of such information will appear from the following discussion of the vertical distribution of the cisco in Trout, Muskellunge, Silver, and Clear Lakes. Particular attention will be given the question of the relationship between the vertical distribution of the cisco and the temperature and oxygen concentration in the different lakes. The data on the vertical distribution of temperature and O₂ in Silver Lake were taken from Juday and Birge (1932, table VI) and those for Trout Lake, Muskellunge Lake, and Clear Lake were supplied by Dr. Chancey Juday from the records of the Wisconsin Geological and Natural History Survey.

The cisco collections from Trout Lake were taken during July, both in 1930 and 1931, and in nets set on the bottom²² at depths of from 15 to 33.5 meters. Nets set anywhere within this region always took good catches of ciscoes while nets set in shallow water (less than 7.5 meters) for the capture of other species caught ciscoes only rarely. The few that were taken in the shallow water nets can be considered stragglers. From the examination of the data of table 39 it can be seen that in Trout Lake in middle and late summer there lies below the depth of 10 or 12 meters a large body of cold water with a good supply of oxygen. It is in this region that the cisco lives during this season of the year, and it is in this region that the samples used for study of density were collected.

TABLE 39.—*Trout Lake, July 1, 1931, and Aug. 27, 1931. Relationship of temperature and dissolved oxygen to depth*

July 1, 1931			Aug. 27, 1931		
Depth in meters	Temperature in °C.	O ₂	Depth in meters	Temperature in °C.	O ₂
0.....	25.4	7.77	0.....	19.9	8.60
5.....	19.4	8.75	5.....	19.9	8.80
10.....	13.5	9.71	10.....	16.8	8.45
15.....	9.5	8.89	15.....	9.8	7.00
20.....	8.3	8.31	20.....	8.4	5.40
25.....	7.6	7.20	25.....	7.8	3.80
28.....	7.5	7.07	28.....	7.6	2.00
31.....	7.3	5.71	31.....	7.3	.66

It is in Muskellunge Lake that the late-summer habitat shows the most marked restriction to a limited stratum. The record of the first three lifts in the 1930 collecting season shows how closely the number of specimens taken depends upon the depth at which the nets are set. On August 27, 1930, nets were lifted in Muskellunge Lake from a depth of 17.5 meters. The total catch was a single sucker. The nets were then reset at a depth of from 7 to 11.75 meters. The catch on August 28 was: 38 perch, 17 suckers, 3 smallmouth black bass, 1 rock bass, and 226 ciscoes. Most of the ciscoes were taken in the nets set at a depth greater than 9 meters. The position

²² It should be remembered throughout these discussions for all lakes that the nets were always set on the bottom at the recorded depths. They actually fished the stratum of water, 3.5 to 6 feet thick, immediately above the bottom.

of the nets was again shifted, this time to depths of 7 meters and shallower. The catch on August 29 was: 60 perch, 13 suckers, 8 smallmouth black bass, 3 rock bass, and only 13 ciscoes. Thus it may be seen that at the end of August 1930, ciscoes occurred on the bottom in abundance only within a rather limited region. They were not plentiful in depths less than 9 meters and were absent in the deeper portion of the hypolimnion.

Most of the ciscoes collected from Muskellunge Lake in 1931 were taken in a single set made July 14 at a depth of 9.5 to 10 meters. Although there are no 1931 data that may be used to set the upper and lower limits of the vertical range of the Muskellunge Lake cisco in that year, nets set at depths less than 8 meters for the capture of other species failed to take ciscoes.

The results of the rather extensive fishing of the 1932 collecting season (table 40) give the most complete information concerning the vertical distribution of the cisco in Muskellunge Lake. From these samples which were taken at different times in July and early August it appears that approximately two-thirds of the fish were captured in nets set at depths between 11 and 13 meters (the fish were taken in the stratum of water 6 feet thick immediately above the bottom). Data on the O₂ and temperature conditions in Muskellunge Lake in the late summer of 1932 based on the results of a vertical series of temperature and O₂ concentration determinations made August 25 (table 41) offer an explanation of the concentration of the cisco into such a narrow stratum and suggest that such a concentration most probably occurs every year. The data of table 41 indicate that in Muskellunge Lake in late summer, oxygen is almost completely lacking in the hypolimnion and may be abundant in the upper part only of the thermocline. As a result of this deficiency of oxygen in the deeper strata the ciscoes are forced out of the cooler strata and by reason of their preference for cool water and their need of oxygen become concentrated in that stratum of water that has the lowest temperature available and yet contains sufficient oxygen to support life.

TABLE 40.—*Muskellunge Lake cisco, 1932—Vertical distribution of the cisco*

[The data show the catch per day's fishing of 100 square yards of gill net, set at different depths. In parentheses are given the number of lifts upon which each average lift was based]

Depth in meters	Size of mesh (in inches)			Depth in meters	Size of mesh (in inches)		
	1¼	1½	1¾		1¼	1½	1¾
Less than 5.....	0.0½ (1)	0.1 (10)	0.1 (9)	11 to 13.....	42.0 (1)	93.4 (5)	0.5 (2)
5 to 7.....	.0 (1)	.1 (9)	.0 (10)	13 to 15.....	1.5 (2)	17.0 (1)	
7 to 9.....	.8 (5)	11.2 (4)	.5 (4)	No depth record.....	21.5 (2)	26.3 (3)	.0 (2)
9 to 11.....	10.3 (6)	29.0 (6)	1.5 (10)				

TABLE 41.—*Muskellunge Lake, Aug. 25, 1932—Relationship of temperature and dissolved oxygen to depth*

[O₂ in milligrams per litre]

Depth in meters	Temperature in °C.	O ₂	Depth in meters	Temperature in °C.	O ₂	Depth in meters	Temperature in °C.	O ₂
0.....	21.3	8.02	10.....	14.5	5.33	15.....	10.5	0.56
5.....	21.3	8.70	11.....	13.8	2.67	19.....	10.1	.24
8.....	20.7	8.25	12.....	12.0	.43			

Because of the heavy concentration of the Muskellunge Lake ciscoes within a narrow stratum in late summer, it is apparent that the catch of ciscoes in a particular net will vary greatly according to the depth at which the net was set. To obviate this difficulty the estimate of the relative density of the population of the Muskellunge Lake cisco was based only on catches of nets set in the depths at which the cisco is most abundant. These depths were 9 to 11 meters in 1930, 9.5 to 10 meters in 1931, and 11 to 13 meters in 1932.

The conditions of life that the Muskellunge Lake cisco finds in middle and late summer in the upper strata of the thermocline are probably far from the optimum for the species. Not only is the water temperature higher than they would normally be expected to select but the crowding itself and the probable competition with the perch that inhabit the same region in large numbers (p. 293) may be expected to make for quite unsatisfactory feeding conditions. In view of these unsatisfactory conditions of life the poor condition (p. 248) of the individuals of this population in contrast to those of other lakes in which chemical conditions are better, and their short life span are not surprising.

That the existence of conditions that force the cisco into unsuitable strata of water may have damaging effects on the population was pointed out by Cahn (1927), who stated that when "the cisco is forced into water far warmer than it ordinarily selects * * * the result is often disastrous", and a high mortality occurs. Scott (1931) showed that where there is formed a "thermocline notch" in the oxygen curve the disappearance of the oxygen from the hypolimnion may force a sudden movement of the ciscoes from the hypolimnion to the upper strata of water. His observations on the cisco of Snow Lake, northeastern Indiana, showed that no great mortality results from this sudden move, but rather that the fish are only temporarily incapacitated. After floating for a short time at the surface they make a recovery and remain in the epilimnion for the remainder of the season. Such a forced removal into an undesirable habitat, either sudden or gradual, doubtless entails considerable shock to the individual fish. It is readily conceivable that a temporary stoppage of growth might occur, and that the occurrence of accessory annuli such as appear in the Muskellunge Lake cisco scales can be thus explained.

The Silver Lake cisco agrees with the Muskellunge Lake cisco in showing a rather sharply delimited vertical distribution. In the summers of both 1930 and 1931 ciscoes were taken only in nets set in depths between 10.5 and 15.5 meters. The dates of collection in 1930 were August 9, 10, and 15; in 1931, July 17 and August 22. The reason for this concentration within a 5-meter stratum appears from the examination of the data of table 42, which shows the relationship between depth and the temperature and O_2 concentration in Silver Lake on August 28, 1931. If the data of table 42 are considered in relation to the known vertical distribution of the cisco in Silver Lake, it would appear that a preference for cool water keeps the ciscoes from entering the warmer strata less than 10 meters deep, while a deficiency of oxygen prevents them from occupying the lower portions of the hypolimnion. Thus in late summer the Silver Lake cisco is confined to a narrow stratum in the upper part of the hypolimnion and the lower part of the thermocline. The catch of nets set between the depths of 10.5 and 15.5 meters can be taken to represent the relative abundance of the Silver Lake cisco at that time.

TABLE 42.—*Silver Lake, Aug. 28, 1931—Relationship of temperature and dissolved oxygen to depth*
[O₂ in milligrams per litre. From Juday and Birge (1932)]

Depth in meters	Temperature in °C.	O ₂	Depth in meters	Temperature in °C.	O ₂	Depth in meters	Temperature in °C.	O ₂
7.....	20.2	9.20	11.....	9.4	9.80	14.....	7.7	1.60
8.....	18.8	9.90	12.....	8.6	7.60	15.....	7.2	.60
9.....	14.7	13.20	13.....	8.2	4.40	18.....	6.8	.00
10.....	11.4	11.70						

The field records of lifts of ciscoes in Clear Lake indicate that in this lake the cisco occurs in all parts of the hypolimnion from midsummer to early autumn. (The dates of collection were July 22 to 28, 1931, Sept. 3 to 5, 1931, and July 12 to 19, 1932.) This distribution of the cisco in Clear Lake suggests that it may at all times find a plentiful supply of oxygen throughout the hypolimnion. Such an assumption is supported by the data on the temperature and dissolved oxygen conditions in this lake based on a vertical series taken August 19, 1932 (table 43). These data show that at this time of the year there is in Clear Lake a plentiful supply of oxygen at all depths. Thus it is valid to assume that the net samples captured at different depths in the hypolimnion may be taken to represent the relative abundance of the cisco in Clear Lake.

TABLE 43.—*Clear Lake, Aug. 19, 1932.—Relationship of temperature and dissolved oxygen to depth*
[O₂ in milligrams per litre]

Depth in meters	Temperature in °C.	O ₂	Depth in meters	Temperature in °C.	O ₂	Depth in meters	Temperature in °C.	O ₂
0.....	20.9	8.07	12.....	12.4	9.46	23.....	8.4	4.51
5.....	20.9	7.91	15.....	9.9	7.93	26.....	8.0	3.25
10.....	18.6	8.07	20.....	8.6	6.03			

The data for the comparison of the relative density of the four cisco populations (table 44) represent the catch of 100 square yards of gill net fished over a period of 24 hours. The lifts upon which the data are based were all made from depths at which the cisco occurred in abundance at the time of capture. These depths include the entire hypolimnions of Trout Lake and Clear Lake and the 10.5–15.5 meter stratum of Silver Lake, while in Muskellunge Lake the depths were 9 to 11 meters in 1930, 9.5 to 10 meters in 1931, and 11 to 13 meters in 1932.

TABLE 44.—*Catch in number of ciscoes per 100 square yards of gill net per 24 hours' fishing*
[Data arranged according to lake, year of capture, and mesh of net]

Lake	Year of capture	Size of mesh						
		1¼	1½	1¾	2	2¼	2½	3
Trout.....	1930.....		104.8					
	1931.....	¹ 61.0	73.0	¹ 1.0	2.8			
	1930.....		106.1					
Muskellunge ²	1931.....		143.9					
	1932.....	¹ 42.0	93.4	¹ .5				
	1930.....		31.6		50.0			
Silver.....	1931.....	¹ 62.0	30.0	¹ 76.0	45.0			
	1931.....	.1	1.4	2.3	3.5	3.7	5.5	7.5
Clear.....	1932.....	.2	.9	1.9	.7	2.4	4.3	3.8

¹ This size of mesh was not represented in the gear of the preceding years.

² The data for the 1932 Muskellunge Lake collections are presented in detail in table 40.

From the examination of the data of table 44 it may be seen that the various populations show considerable differences in their relative densities at the time of capture in the depths from which the samples were taken. The Muskellunge Lake fish appear to be the most abundant although Trout Lake is not far behind. The Silver Lake data show a relative abundance slightly less than that in Trout Lake or Muskellunge, while the Clear Lake cisco population may be considered relatively sparse.

The estimate of the relative densities of the four cisco populations at the time of capture is not, however, of primary importance in this investigation. Since this section is concerned chiefly with the relationship between density of population and rate of growth the most significant comparison of population densities must include a comparison of densities throughout the entire growing season rather than at some particular time within the growing season. It was pointed out in the section on the length of the growing season that growth of the Trout Lake cisco is practically complete at the end of July; the Muskellunge cisco completes its growth by the end of August, possibly sooner; the season's growth of the Silver Lake fish is two-thirds to three-quarters complete in mid August; and the Clear Lake cisco has completed well over half its season's growth by late July. From these facts it is apparent that the relative density of the four populations in late spring and the first half of the summer is more significant than their relative densities at the time the samples were collected. There is strong evidence that in Muskellunge Lake and Silver Lake at least the densities of the cisco populations earlier in the growing season were less than at the time of capture in late summer. The concentration of these populations in late summer within a narrow stratum may be considered the result of the temperature and oxygen condition at that time. It is most probable that in late spring and early summer no such concentration existed, since in the early season oxygen would be expected to occur at all depths in the hypolimnion. Consequently the relative densities for the Muskellunge Lake and Silver Lake fish in table 44 must be considered too high as compared to those from Trout Lake and Clear Lake.

If attention is given to the relative densities during the entire growing season the most probable arrangement of the lakes from the most dense to the least dense population is: Trout, Muskellunge, Silver, Clear. This is the same order these lakes show with respect to growth rate in weight (with slowest growth in Trout Lake and fastest growth in Clear Lake). The growth rates of the four populations are approximately in the reverse order of the productive capacities of the lakes as estimated from the amount of bound CO_2 in their waters (Clear Lake was estimated as the least productive, followed in order by Muskellunge, Silver, and Trout). Thus it appears that the growth rates of these populations are determined primarily by their relative densities rather than by the basic productive capacities of the waters they inhabit. Although it is recognized that crowding itself may possibly impede growth to a certain extent independently of its effect in creating competition for food, and that various physical-chemical factors may affect growth rate directly, it is believed that the differences in growth rate in these four populations depend in large measure on the varying degrees of competition for food in the different lakes. It is further probable that variation in the intensity of competition for food from lake to lake may be related to the observed differences in the length of the growing season of the different stocks. (See preceding section.)

AGE COMPOSITION OF THE SAMPLES AND THE RELATIVE ABUNDANCE OF YEAR CLASSES

Because of its importance in the study of commercial fisheries the question of age composition of the stock and of the existence of dominant year classes has in recent years received a great amount of attention. It is now well known that the success of different years' hatches as measured in terms of the number of young produced is subject to a wide range of variation from one year to another. The hatches of some years may be so successful that that particular year class may dominate in the fishery over a period of 1 or several years. Yet other hatches may be so unsuccessful as to make only minor contributions to the stock. The common occurrence of relatively successful and unsuccessful year classes has been demonstrated in many species of fish of commercial importance. The study of the age composition of the commercial catch over a period of years has served as a most valuable tool in the investigation of fluctuations in abundance. In both Europe and America the known age composition of the commercial stock, together with the observed rate of falling off of a year group from year to year, has been used by fisheries investigators as a basis of prediction of the probable yield of the fishery for the approaching season.

In spite of the extensive researches that have been made on the subject of fluctuations little is known as to the causes that make a year class good or bad. Hjort (1914) stated that while the basic causes of fluctuations in abundance are unknown, it appears that fluctuations "have their origin in certain conditions prevailing at a very early period in the life of the fish." He repeated this opinion in 1926. Storrow (1932) pointed out that not only are the factors that determine the success or failure of a year class complex, but also that the difficulty of observing the fish in its natural environment is great. He called attention further to the failure of attempts to simulate natural conditions in the laboratory, a convincing proof of inadequate knowledge of optimum conditions.

The most thorough-going studies on the question of fluctuations in abundance in coregonids and their causes are those of Järvi (1920, 1924, 1930). He was able to show not only a great variation in the abundance of different year classes of the "kleine Maräne" (*Coregonus albula*) but also a distinct connection between such variations in abundance and weather conditions in the spring just after the time of hatching. If there are strong winds at this critical period many of the delicate newly hatched young are destroyed by the wave action. Järvi found, however, that strong winds at the time of spawning are less harmful.

Huitfeldt-Kaas (1917) found that in some years in Lake Mjøsen almost all the spawning run individuals of *Coregonus albula* are taken in the commercial fishery before they have had an opportunity to spawn, and that poor year classes may result.

Because of the manner (collecting with gill nets) in which the samples were obtained in the present investigation the study of the relative abundance of the various age groups in the four cisco populations and along with it the consideration of the relative abundance of the different year classes must be approached with great caution. (The limitations of gill net samples in the study of relative abundance of age groups and year classes are discussed in the section on the selective action of gill nets.) The age composition of a gill-net sample must in general be considered as descriptive of the sample rather than of the population as a whole. Exceptionally, however, the representatives of some particular year class may appear so prominently or be so scarce at all of the ages at which that year class appears in different

collecting years that it may be possible to designate the year class as good or poor. The examination of the age composition of the different years' collections in each of the four lakes (tables 45 to 48) does indicate the presence of certain year classes that can be termed relatively good or relatively poor.

In the Trout Lake collections (table 45) the year classes of 1926 and 1927 appear to represent good years for the production of young. The former year class as the II group of 1928 made up more than half of that year's collection, and 3 years later as the V group of 1931 it was still relatively abundant, comprising 13 percent of the total collection in this latter year. By reason of gear selection the 1927 year class (I group of 1928) was almost entirely lacking in the 1928 collections. This year class was, however, dominant in the collections of the later years, first as the III group of 1930 and then as the IV group of 1931. These conclusions as to the "goodness" of the 1926 and 1927 year classes are supported by the comparison of the relative abundance of corresponding age groups in the different years' collections. The 1926 year class furnished the greatest relative abundance of any II group in any year ²³ (56.0 percent of 1928 collection) and also of any V group (13.0 percent of the 1931 collection). Similarly the 1927 year class furnished the greatest relative abundance of any III group (1930) and of any IV group (1931). It should be mentioned further that the presence of these two relatively successful groups contributed toward the progressive increase from year to year in the average age and average size of the fish in the collections obtained from Trout Lake.

TABLE 45.—*Age composition of the samples of the Trout Lake cisco*

[The percentages are given in parentheses]

Year of capture	Age											
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
1928.....	2 (1.1)	102 (56.0)	61 (33.5)	17 (9.3)	-----	-----	-----	-----	-----	-----	-----	-----
1929.....	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
1930.....	-----	36 (9.2)	247 (63.2)	99 (25.3)	9 (2.3)	-----	-----	-----	-----	-----	-----	-----
1931.....	2 (0.3)	61 (10.0)	173 (28.4)	269 (44.1)	79 (13.0)	12 (2.0)	4 (0.7)	5 (0.8)	2 (0.3)	-----	2 (0.3)	1 (0.2)

In the Muskellunge Lake collections (table 46) the year class of 1928 (II group of 1930, III group of 1931) may be considered relatively successful. This year class, as the III group composed 55.6 percent of the 1931 collections, whereas in preceding years the III group composed a negligible portion of the total collection. The similarity of the age composition of the 1928 and the 1930 collections suggests the possibility that the 1926 year class may have been exceptionally abundant and that a collection in 1929 would have shown a high percentage of III-group individuals. However, the almost total absence of all age groups above the II group in the 1928 and 1930 collections suggests also the possibility that heavy mortality may regularly reduce the numbers of Muskellunge ciscoes early in life, and that the great relative abundance of the III group in 1931 may depend not only on the great relative abundance of the 1928 year class but also in part on the failure of this year class to suffer this customary great mortality. The scarcity of I-group individuals in all Muskellunge Lake collections may be considered the result of selectivity by gear.

²³ The great abundance of II-group fish in 1928 may depend in part on the smaller mesh gill nets used in that year.

TABLE 46.—*Age composition of the samples of the Muskellunge Lake cisco*

[The percentages are given in parentheses]

Year of capture	Age			
	I	II	III	IV
1928.....	19 (6.8)	252 (89.7)	10 (3.6)	-----
1929.....	-----	-----	-----	-----
1930.....	17 (6.9)	214 (87.3)	14 (5.7)	-----
1931.....	9 (1.5)	258 (41.9)	347 (55.3)	2 (0.3)

The study of the age composition of the Silver Lake collections (table 47) reveals the presence of one year class (1926) which may be considered good and of one year class (1929) which may be considered poor. The 1926 year class was dominant in the collections of 2 of the 3 years, as the IV group of 1930 and as the V group of 1931. The scarcity of 1926 year class individuals as the II group in the 1928 collection can be explained on the basis of gear selectivity. The 1929 year class must be considered relatively poor because of its relative scarcity as the II group of the 1931 collections. This scarcity can hardly be the result of selection by gear as the individuals of the age groups on either side are more than three times as numerous. The great abundance of I-group fish in 1931 as compared with 1930 is the result of the introduction of smaller meshed nets in the first-named year. The lack of individual net records makes it impossible to determine the reason for the scarcity of I-group fish in 1928. However, the 1930 year class can safely be considered more abundant than the 1929 year class. The 1924 year class which was dominant as the 1928 IV group may possibly represent a good production year.

TABLE 47.—*Age composition of the samples of the Silver Lake cisco*

[The percentages are given in parentheses]

Year of capture	Age						
	I	II	III	IV	V	VI	VII
1928.....	1 (0.7)	9 (6.7)	46 (34.1)	69 (51.1)	10 (7.4)	-----	-----
1929.....	-----	-----	-----	-----	-----	-----	-----
1930.....	-----	7 (5.9)	25 (21.2)	58 (49.2)	25 (21.2)	3 (2.5)	-----
1931.....	66 (17.5)	19 (5.0)	61 (16.1)	102 (27.0)	108 (28.6)	21 (5.6)	1 (0.3)

The Clear Lake samples (table 48) present much more definite and consistent indications of the presence of successful and unsuccessful year classes than were found in the other three lakes. Figure 5 shows graphically the year class composition for the 1931 and 1932 collections. The agreement between the 2 years in the relative abundance of the different year classes is close. Since the individuals of each year class were a year older in 1932 than in 1931, and consequently of a different size range, this close agreement between the year class composition of the 2 years' collections may be taken as strong evidence for a high degree of reliability of the Clear Lake samples both as to year class and as to age composition.

TABLE 48.—Age composition of the samples of the Clear Lake cisco

[The percentages are given in parentheses]

Year of capture	Age										
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
1931.....	38 (15.3)	69 (24.5)	51 (20.5)	14 (5.6)	6 (2.4)	23 (9.2)	29 (11.6)	16 (6.4)	1 (0.4)	2 (0.8)	-----
1932.....	31 (16.2)	33 (17.3)	44 (23.0)	25 (13.1)	14 (7.3)	3 (1.6)	21 (11.0)	15 (7.9)	3 (1.6)	1 (0.5)	1 (0.5)

It can be seen at once from the examination of table 48 and figure 5 that in Clear Lake the 1926 year class (V group of 1931, VI group of 1932) was very unsuccessful,

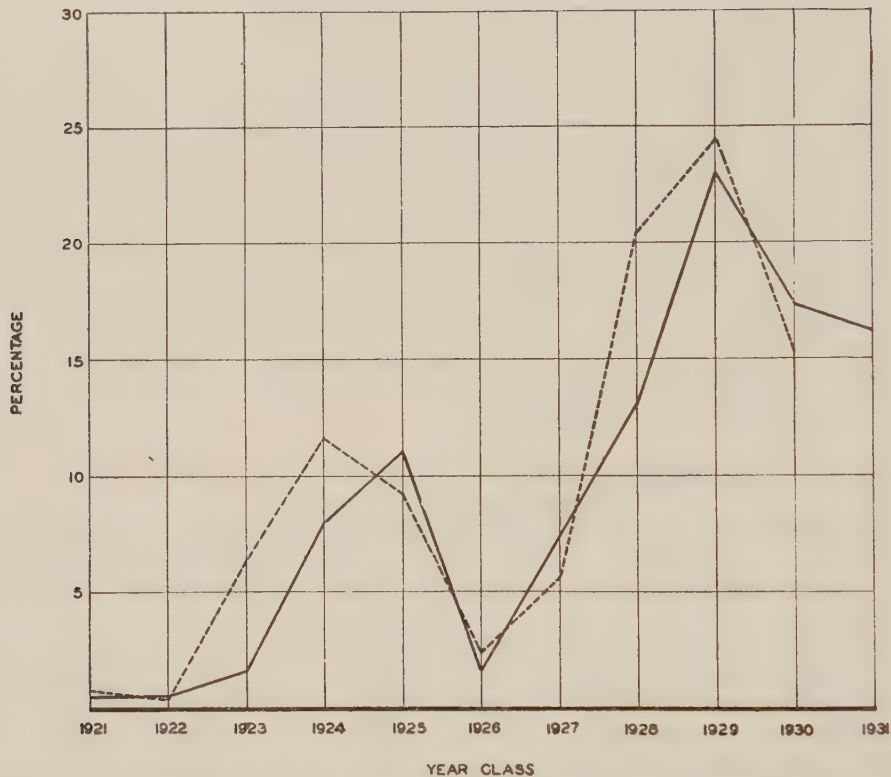


FIGURE 5.—Percentage representation of the different year classes in the Clear Lake cisco collections. 1931, broken line; 1932, solid line.

while the 1929 year class (II group of 1931, III group of 1932) which was dominant in the collections of both years may be termed good. It can be considered valid to state further that the 1924 and 1925 year classes (VII and VI groups of 1931) and probably the 1928 year class (III group of 1931) were more successful than those of 1926 and 1927 (V and IV groups of 1931), and that the 1929 year class (II group of 1931) was more successful than either that of 1930 (I group of 1931) or 1931 (I group of 1932).²⁴

In the comparison of the relative abundance of different year classes in Clear Lake some consideration should be given the matter of the age of the samples upon

²⁴ In contrast to the other 3 populations the I-group samples of Clear Lake can be considered representative. (See the section on "The selective action of gill nets.")

which the estimations are based. For example, the 1927 year class which as the IV group composed 5.6 percent of the 1931 collection and as the V group composed 7.3 percent of the 1932 collection must be considered to represent a much less successful year than the 1924 year class which as the VII group of 1931 composed 11.6 percent of that year's collection and a year later as the VIII group made up 7.9 percent of the 1932 collection. Although the 1924 year class individuals in both years' collections combined were only about one and one-half times as numerous as those of the 1927 year class, the former year class, by reason of its 3 years greater age, had suffered the reducing effect of natural mortality over a longer period of time. Consequently the 1924 year class as compared with the 1927 year class may be considered much more successful than the comparison of the representation of the two groups in the collections would indicate. A similar line of reasoning leads to the conclusion that the 1925 year class (VI group of 1931) also represents a very successful year. The same conclusion may possibly apply to the 1923 year class which was well represented as the VIII group of 1931.

In the preceding discussion it was shown that in each population there existed a considerable variation in the numerical abundance or successfulness of the various year classes. The years that appear to have had a production of relatively successful year classes were: Trout Lake—1926, 1927; Muskellunge Lake—1928; Silver Lake—1926; Clear Lake—1924, 1925, 1929. In Silver Lake the 1929 year class was poor, and in Clear Lake the 1926 and 1927 year classes must be considered relatively unsuccessful.

Since the four populations show no agreement in the matter of goodness or poorness of the various year classes, it may be concluded that in each population the success of the individual year classes depends on the purely local conditions within the lake. This conclusion is of particular interest in view of the rather general opinion that fluctuations in the relative abundance of year classes have their origin in differences in weather conditions from one year to another. Inasmuch as these four lakes are grouped closely together (the maximum distance between any two of them is about 18 kilometers) they must all be subjected to approximately the same weather conditions.

It must be remembered that relative abundance is not a wholly reliable index of absolute abundance. A poor year class may appear quite numerous in comparison to a yet poorer one. Järvi (1920) gave an excellent illustration of this fact when he pointed out that the great relative abundance of third year fish in some years' catches of the "kleine Maräne" depended not upon the actual abundance of that particular age group but was rather the result of the scarcity of fish in their second year of life.

The data of tables 45 to 48 make possible a comparison of longevity in the four populations. The Muskellunge Lake cisco has definitely the shortest average life span. The Trout Lake cisco falls second and the Silver Lake cisco third, while the average life span of the Clear Lake cisco is quite long. A possible explanation of these differences among the four populations as to the average length of life was mentioned in the section on condition in the different populations.

AGE AT MATURITY AND SEX RATIO

Although the collections of the cisco were made in July, August, and early September, several months before the time of spawning in November, the development of the gonads was such as to leave little doubt as to the sexual maturity of the

individual. Fish that would have spawned the following autumn could be distinguished easily from those which would not have spawned at that time. The former were considered here as matured fish even though they may not have spawned previously.

Sexual maturity occurs at an early age in each of the four populations. All the Clear Lake fish with the exception of a few I-group individuals were mature or maturing. Since there is good reason to believe that the I-group samples from Clear Lake are representative, it may be concluded that in this population the first spawning occurs in the autumn of the second year of life. Practically all the I-group individuals in the samples from Trout, Muskellunge, and Silver Lakes would have spawned the following autumn. There is reason to believe, however, that in these populations the nets used for collecting the samples took only the larger I-group individuals. The smaller members of the age group may have been immature. In all three populations, however, all II-group individuals indicated that they would spawn in the autumn.

The ciscoes of the four populations considered in this investigation attain sexual maturity at an earlier age than has been found by some investigators of this species. Clemens (1922), referring to *L. artedi* in Lake Erie, stated that first spawning is "probably at the end of the third summer." The ciscoes of the inland lakes of southern Wisconsin spawn at the age of 3 years (Cahn 1927). Van Oosten (1929) found that in the Saginaw Bay herring only a few fish matured in the second year, and that the majority matured in the third and fourth years of life. Van Oosten's data were based on the examination of individuals from the spawning run. In the Lake Ontario cisco Pritchard (1931) found a few females but no males mature at 2+ years. He stated further that several individuals of both sexes were mature at 3+ years, while spawning was general at 4+ years. Dymond (1933) found that in Hudson Bay the cisco does not mature "until the fourth and probably the fifth year."

The sex ratio expressed as the number of females per 100 males was determined by age groups for each of the four populations. These data are presented in table 49.

TABLE 49.—Sex ratio according to age in each of the four populations

[The ratio is expressed as the number of females per 100 males. The numbers of specimens are shown in parentheses. The age groups which were composed entirely of one sex are indicated by the sex symbols. The Clear Lake data were obtained by combining the 1931 and 1932 collections. The data for the remaining three lakes are based on the combination of the 1930 and 1931 collections]

Lake	Age					
	I	II	III	IV	V	VI
Trout.....	100 (2)	162 (97)	204 (520)	354 (368)	1,367 (88)	1,100 (12)
Muskellunge.....	100 (26)	130 (472)	151 (361)	♂ (2)	-----	-----
Silver.....	110 (66)	160 (26)	126 (86)	111 (160)	129 (133)	200 (24)
Clear.....	72 (60)	89 (102)	94 (95)	86 (39)	82 (20)	100 (26)

Lake	Age						Average
	VII	VIII	IX	X	XI	XII	
Trout.....	♀ (4)	400 (5)	♀ (2)	-----	♂ (2)	♀ (1)	267 (1,101)
Muskellunge.....	-----	-----	-----	-----	-----	-----	137 (861)
Silver.....	♀ (1)	-----	-----	-----	-----	-----	124 (496)
Clear.....	194 (50)	210 (31)	300 (4)	♀ (3)	♀ (1)	-----	104 (440)

With the exception of the irregular data of Silver Lake, the females tend to become relatively more abundant as age increases. The tendency toward a progressively greater preponderance of females finds an extreme condition in Trout Lake where male individuals are rare beyond the IV group. The Clear Lake fish differ from those of the other three lakes in that the males outnumber the females in the first five age groups. In the VI group the numbers are equal while in the age groups above 6 years the females are much more numerous than the males. Differences among the populations in the rate of change of the sex ratio with increased age are reflected in the average sex ratio for each population as based on the combination of all age groups.

It is believed that the data of table 49 are a reliable index of the sex composition of the four populations. Cahn (1927) and Van Oosten (1929) pointed out that males arrive at the spawning ground earlier than the females. European investigators of coregonids have observed frequently that not only do males arrive at the spawning grounds earlier than females but that they remain there longer. As a consequence, if samples are taken from the spawning run the conclusions concerning the sex ratio would not only be affected by the time within the spawning period of the taking of the sample but also would tend to contain a too high percentage of males. The collections used in this investigation are not open to such a criticism. All samples were taken during the summer, several months before the spawning time, and there is no evidence pointing toward a segregation of the sexes at this period of the year.

The data relative to the sex ratio in the four populations differ from those given by Cahn (1927) for the lakes, Mendota and Oconomowoc, in southern Wisconsin and by Van Oosten (1929) for the Lake Huron herring. Cahn found 101 males and 62 females in his collections from Lake Mendota and 429 males as against 315 females in his samples from Oconomowoc Lake. He combined the collections from the two lakes to obtain a ratio of 100 males to 71.2 females. Cahn attributed the greater abundance of males to the relatively higher mortality of the females during the warm weather of late summer. His data on sex ratio were not correlated with age.

Van Oosten (1929) found males and females approximately equally abundant (49.5 percent males) in his samples of the Lake Huron herring taken at Bay City, Mich. He did, however, find differences in the sex ratio in the different age groups. Females were the more numerous in the younger age groups (I and II in the method of age designation used in this paper) while the males were the more abundant in the older age groups. Van Oosten attributed the shifting sex ratio to an earlier attainment of sexual maturity on the part of the females and a consequent tendency for them to appear in the commercial catch at an earlier age.

The change with age in the sex ratio of the four cisco populations of this study must be explained on the basis of a differential mortality of the two sexes. Since there is no fishery for the cisco in these lakes, there can be no disturbance of the natural relationship through the catching of more individuals of the one sex than of the other. The reason for the observed differences in differential mortality in the four lakes presents a problem difficult of explanation. Attention should be called to the fact that with respect to the relative abundance of males in the entire samples the lakes fall in the same order that they show with respect to the amount of growth in weight, that is the population with the slowest growth (Trout Lake) has relatively fewest males. The possible significance of this parallelism will be considered later.

Willer (1929) suggested that selective destruction by carnivorous forms might affect the sex ratio in the kleine Maräne (*Coregonus albula*). In the younger groups the heavier, less agile female would fall prey to predators more readily than the males. In the older groups the heavier females would be protected by virtue of their size as the predatory fish would select the slenderer males as prey of more suitable proportions. Such an assumption does not serve to explain the change with increase in age in the sex ratio of the four populations of the present investigation. Though the Trout Lake stock shows the most rapid shift toward a preponderance of females, the growth of the two sexes in this lake is the same both with respect to length and weight. Furthermore, the greatest changes in sex ratio occur between age groups that show only slight differences in average length and weight. The situation in Muskellunge Lake is similar to that in Trout Lake. In Silver Lake the males tend to be slightly heavier than females of the same age while in Clear Lake the females are distinctly heavier than the males. Yet in both populations, particularly in the Clear Lake cisco, females are relatively more abundant than males in the older age groups.

In view of the fact that the greatest progressive change in the sex ratio with increase in age occurs in the population in which there is least reason to expect selection on the basis of sex by the carnivorous forms which prey on that population, it must be concluded that the differential mortality upon which the changing sex ratios depend is not the result of selection by predators. The differential mortality of the two sexes is probably the result of basic differences in their innate physiological mechanisms, differences that vary in their manifestations from one population to another, and whose effects appear to be associated to some extent with the growth rate of each particular population.

The above suggestion of an explanation of the differential mortality of the sexes of the cisco is in agreement with the conclusions of Geiser (1923, 1924, a, b,) ²⁵ who held that females are inherently better fitted than males to survive adverse environmental conditions. The explanation of the sex ratio on these grounds assumes particular interest when it is considered in relationship to the correspondence between sex ratio and growth rates in the four cisco populations of this study. It was pointed out (p. 269) that in these populations slow growth is associated with a relative paucity of males. It appears logical to assume that the environmental factors that doubtless contributed to the observed differences in growth rate may at the same time have produced corresponding differences in the sex ratios of these same populations. Thus the very slow growth of the Trout Lake cisco may be associated with very adverse environmental conditions that also produce an exceptionally high mortality among the less viable males. This excessive mortality of males as compared to females would produce the observed rapid change with increased age in the sex ratio and the relatively high abundance of females in the population as a whole. Similarly, the better growth in Muskellunge Lake and Silver Lake may be taken to represent conditions less adverse than those in Trout Lake. In these less adverse environments of Muskellunge and Silver Lakes the mortality of males as compared to females is less than in Trout Lake, and females are relatively less abundant in the populations as a whole. Finally, the favorable conditions that permit such excellent growth in the Clear Lake cisco are reflected in the slowly changing sex ratio and the almost equal representation of the two sexes in that population.

²⁵ In these papers Geiser included comprehensive reviews of the literature on the subjects of sex ratios and differential mortality of sexes, not only in the fishes but in other animal groups as well.

ANNUAL INCREMENTS OF GROWTH

VARIATION IN THE AMOUNT OF GROWTH IN DIFFERENT CALENDAR YEARS

Tables 50 to 54 show the calculated annual growth increments for each of the best represented age groups in the collections of each cisco population. (In Clear Lake all age groups below the IX group were included.) The arrangement of the tables is such that each horizontal row shows the growths in different calendar years of fish of the same age and in the same year of life. The vertical columns show growth increments for the same calendar year but for fish that are either of different age or in different years of life, sometimes both. Each diagonal row shows the growth increments in the different calendar years of a single age group in a single year's collection. The calendar year corresponding to the first year of life of any particular age group is the year of birth, while the year of capture of each age group is one year later than the calendar year of the last growth increment shown in the table for that age group.

TABLE 50.—Annual calculated growth increments in millimeters of the Trout Lake cisco, ages III to V, according to calendar year and year of life

Age	Year of life	1924	1925	1926	1927	1928	1929	1930	Average
V	5						12	9	10.5
	4					13	10		11.5
	3				19	17			18.0
	2			34	37				35.5
IV	1		82	81					81.5
	4				10		10	11	10.3
	3			13		19	20		17.3
	2		35		36	37			36.0
III	1	85		82	78				81.7
	3				14		22	17	17.7
	2			39		38	36		37.7
	1		84		79	84			82.3

TABLE 51.—Annual calculated growth increments in millimeters of the Muskellunge Lake cisco, ages II and III, according to calendar year and year of life

Age	Year of life	1925	1926	1927	1928	1929	1930	Average
III	3			20		25	18	21.0
	2		37		47	49		44.3
	1	105		85	96			95.3
II	2			48		48	40	45.3
	1		99		95	98		97.3

TABLE 52.—Annual calculated growth increments in millimeters of the Silver Lake cisco, ages II to VI, according to calendar year and year of life

Age	Year of life	1923	1924	1925	1926	1927	1928	1929	1930	Average
VI	6							15	12	13.5
	5						16	19		17.5
	4					27	16			21.5
	3				22	23				22.5
	2			40	41					40.5
V	1		72	78						75.0
	5					14		20	14	16.0
	4				19		20	18		19.0
	3			27		25	24			25.3
	2		39		46	46				43.7
IV	1	76		74	80					76.7
	4					16		21	17	18.0
	3				25		26	27		26.0
	2			46		48	52			48.7
III	1		79		78					79.0
	3					80		33	29	80.7
	2				54		57	54		55.0
	1			73		77	83			77.7
II	2					60		52	47	49.7
	1				90		99	104		97.7

TABLE 53.—Annual calculated growth increments in millimeters of the Clear Lake cisco (males), age groups I to VIII, according to calendar year and year of life

Age	Year of life	1923	1924	1925	1926	1927	1928	1929	1930	1931	Average
VIII.....	8								7	11	9.0
	7							12	13		12.5
	6						17	16			16.5
	5					18	23				20.5
	4				31	29					30.0
	3			45	55						50.0
	2		85	87							86.0
	1	118	108								113.0
VII.....	7								12	13	12.5
	6							14	16		15.0
	5						19	22			20.5
	4					30	32				31.0
	3				51	60					55.5
	2			88	86						87.0
	1		110	102					13	16	106.0
	6								13	16	14.5
VI.....	5							21	16		18.5
	4						34	32			33.0
	3					56	68				62.0
	2				84	85					84.5
	1			108	98						103.0
	5								22	24	23.0
	4							43	39		41.0
	3						58	68			63.0
V.....	2					79	83				81.0
	1				110	98					104.0
	4								34	42	38.0
	3							68	69		68.5
	2						86	86			86.0
	1					104	105				104.5
	3								67	70	68.5
	2							84	88		86.0
III.....	1						104	110			107.0
	2								92	105	98.5
	1							108	113		110.5

TABLE 54.—Annual calculated growth increments in millimeters of the Clear Lake cisco (females), age groups I to VIII, according to calendar year and year of life

Age	Year of life	1923	1924	1925	1926	1927	1928	1929	1930	1931	Average
VIII.....	8								11	12	11.5
	7							13	15		14.0
	6						15	20			17.5
	5					22	26				24.0
	4				33	32					32.5
	3			54	52						53.0
	2		87	89							88.0
	1	112	106								108.5
VII.....	7								13	18	15.5
	6							17	17		17.0
	5						23	28			25.5
	4					32	42				37.0
	3				54	62					58.0
	2			88	82						85.0
	1		108	108							108.0
	6								16	16	16.0
VI.....	5							28	16		22.0
	4						42	32			37.0
	3					58	68				63.0
	2				78	85					81.5
	1			105	98						101.5
	5								24	32	28.0
	4							44	46		45.0
	3						70	74			72.0
V.....	2					80	79				79.5
	1				108	98					103.0
	4								33	44	38.5
	3							82	73		77.5
	2						88	92			90.0
	1					103	103				103.0
	3								70	77	73.5
	2							91	97		94.0
III.....	1						108	108			108.0
	2								92	105	102.0
	1							108	114		111.0

The examination of tables 50 to 54 shows that the amount of growth made by fish of the same age and in the same year of life varies considerably from one calendar year to another. This variation is doubtless to a certain extent random and of no particular significance. In each population, however, there may be detected certain calendar years that by reason of the consistently good or poor growth made in them may be considered good or poor growth years. For example, the growth of the Silver Lake cisco and the Muskellunge Lake cisco (possibly that of the Trout Lake cisco also) appears to have been better than average in the year 1929 while the Clear Lake cisco shows excellent growth for 1931. On the other hand, growth in the first three of the above populations appears to have been relatively poor in 1930, while the Clear Lake cisco shows poor growth for 1926 and 1927 at least.

The relative positions of the different calendar years with respect to goodness or poorness of growth may be brought out more clearly by simple methods of analysis. In the Trout Lake, Muskellunge Lake, and Silver Lake cisco populations the relative position of each calendar year was determined on the basis of the percentage deviation from average growth in that particular year. As an illustration of the method of determining the deviation from average growth consider the growth of the Silver Lake cisco in the calendar year 1924 (table 52). The calculated first year growth of 72 millimeters of the VI group (year class of 1924) represents a -4.0 percent deviation from the average of 75-millimeter growth for VI-group fish in the first year of life; the 39-millimeter growth of the V group (1923 year class) in its second year of life represents a -10.8 percent deviation from the average growth of 43.7 millimeters for V-group fish in the second year; and finally the 79-millimeter first year's growth of the III group (year class of 1924) represents a 0.0 percent deviation from the average of 79-millimeter growth for III-group fish in the first year of life. The mean of these three deviations is -4.9, and it may be considered that the growth of the Silver Lake cisco in 1924 was 4.9 percent below average. The deviations from average growth for each calendar year calculated by the above method are shown in table 55 for Trout, Muskellunge, and Silver Lakes.

TABLE 55.—*Percentage deviation from average growth in the different calendar years*

Lake	Calendar year								
	1923	1924	1925	1926	1927	1928	1929	1930	1931
Trout.....		4.0	0.0	-5.2	-3.2	3.8	5.6	-4.2	-----
Muskellunge.....			10.2	-7.4	-3.2	1.4	9.1	-13.0	-----
Silver.....	-0.9	-4.9	-0.9	-0.7	-0.5	-1.7	7.7	-8.0	-----
Clear.....	3.3	-4.1	-5.1	-8.5	-8.5	-0.4	3.2	3.1	17.1

In criticism of the above method of determining the relative position of the different calendar years as to the amount of growth, it should be mentioned that the evaluation of the different years depends on comparisons that are based on different combinations of year classes and age groups, and that the evaluation of a single calendar year is based not upon a single comparison with all other calendar years involved but rather is the average of a group of comparisons no one of which involves more than 3 calendar years. If one of these single comparisons should happen to involve, for example, 3 poor-growth years the resultant percentage deviations would give too high an estimate of the relative goodness of these growth years as compared to calendar years not involved in the comparison. Similarly, a comparison that involves 3 good-growth

years will give too low an estimate of the goodness of growth in these years as compared with years not involved in this particular comparison. The possible distorting effect of examples such as those just given is obviated in large measure, however, by the fact that the evaluation of the goodness of growth of a single year involves comparisons with so many other calendar years that the effect of a single distorted comparison will tend to be greatly reduced.

In Silver Lake (table 52), for example, the evaluation of the year 1927 is based on comparisons that involve all other years from 1924 to 1930, inclusive. At the best, however, the evaluation of growth in different calendar years shows only their relative positions, and a general shifting of values might be expected to follow the

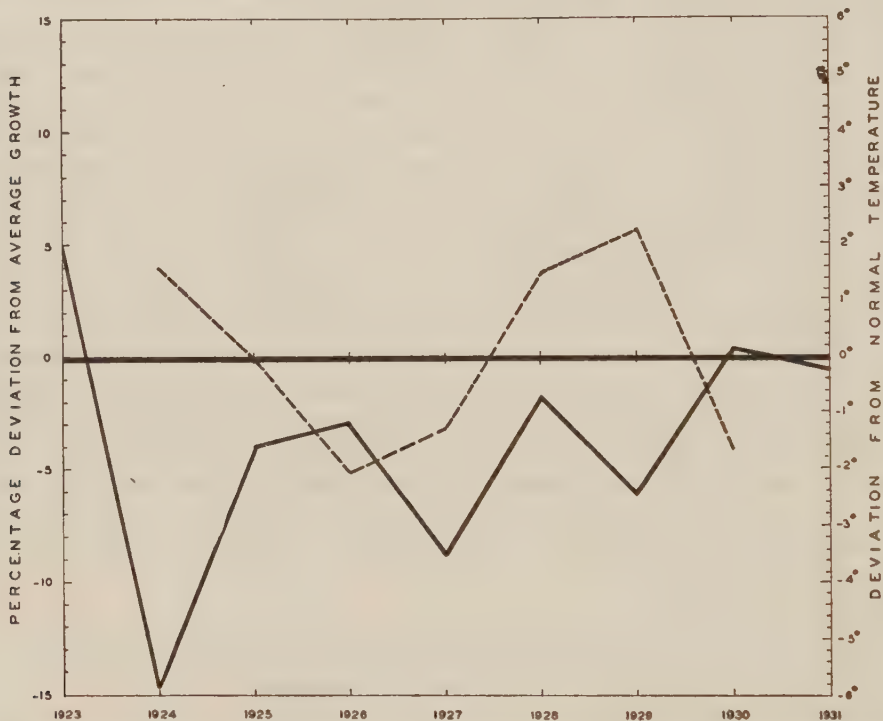


FIGURE 6.—Relationship in different calendar years between the deviation of the growth of the Trout Lake cisco from the average and the deviation of the air temperature from the normal during the cisco's growing season. Deviation from the average growth, broken line; deviation from normal temperature, solid line.

elimination or addition of another calendar year in the comparisons. The method of comparing goodness of growth in Trout, Muskellunge, and Silver Lakes in different calendar years has the advantage that all the single comparisons are based on fish of the same age, and that any possibility of a distortion through Lee's phenomenon is thereby eliminated.

The fact that collections of the Clear Lake cisco were made in only 2 consecutive calendar years makes necessary a slightly different procedure in the comparison of growth in that lake in different calendar years. In Clear Lake the evaluation of the goodness of growth by the method employed in the other three populations would mean that the estimate of the relative position of a single calendar year would be based not on comparisons with several other calendar years but on comparisons with only the single years immediately preceding and immediately following the year in

question. Since, as will be brought out presently, the calendar years 1924 to 1927, inclusive, were all below average as to goodness of growth, while the years 1929, 1930, and 1931 were all above average, the limitation of the estimate for a poor year, as for example 1926, to comparisons with two other poor years, 1925 and 1927, or of a good year as 1930 to comparisons with other good years, 1929 and 1931, would lead inevitably to erroneous conclusions concerning the goodness of growth in these years. To avoid this difficulty the evaluation of the different years was based on the comparison of total growth in each calendar year with that of the preceding year.

An illustration will be given of the method used in the evaluation of goodness of growth of the Clear Lake cisco in different calendar years. (See table 53.) In 1924

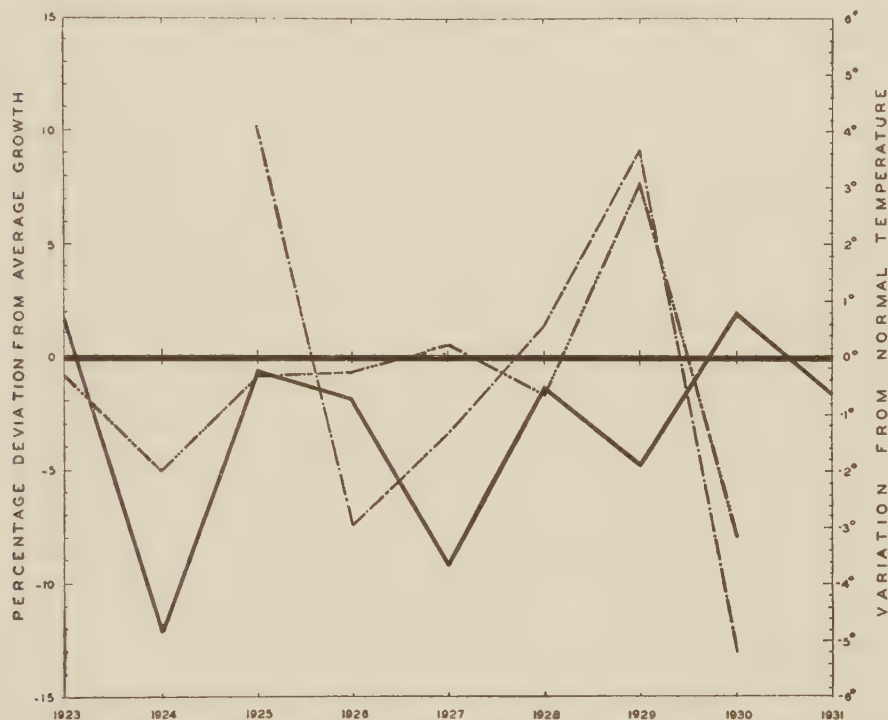


FIGURE 7.—Relationship in different calendar years between deviation of growth of Muskellunge Lake cisco and of Silver Lake cisco from average, and deviation of air temperature from normal during cisco's growing season. Deviation from average growth, Muskellunge Lake cisco — — —; Silver Lake cisco — . . . —; deviation from normal temperature, — — —.

the first year's growth of the VIII-group fish was 108 millimeters. This growth was 10 millimeters or 8.5 percent less than the first year's growth of the preceding year (118 millimeters in 1923). Thus the calendar year 1924 shows a —8.5-percent deviation from 1923 as to goodness of growth. Similarly the 1925 growths of 87 (VIII group, second year of life) and 102 (VII group, first year of life) show a total of 189 or a deviation of —3.1 percent from the total corresponding growth of 195 millimeters in 1924. The position of 1925 with respect to 1923 is the sum of the deviations, —8.5 and —3.1 or —11.6 percent. A continuation of this procedure shows the position of each calendar year with respect to the year, 1923. In order to make the relative positions of the different years describe their deviations from average growth rather than from 1923 growth, the mean value of all the deviations as computed from 1923 as the starting point was subtracted from the individual devia-

tion of each year. The final figures after a combination of the sexes (table 55) indicate that growth in 1923 was 3.3 percent above average. Although the Clear Lake data of table 55 were obtained by a different method from the data pertaining to the other three lakes, the fact that all these "deviations from average growth" are used only to show relative positions of the different calendar years makes a comparison of the data of all four lakes valid.

The data of table 55 are presented graphically in figures 6 to 8. The examination of the curves reveals a certain degree of correspondence as to goodness or poor-

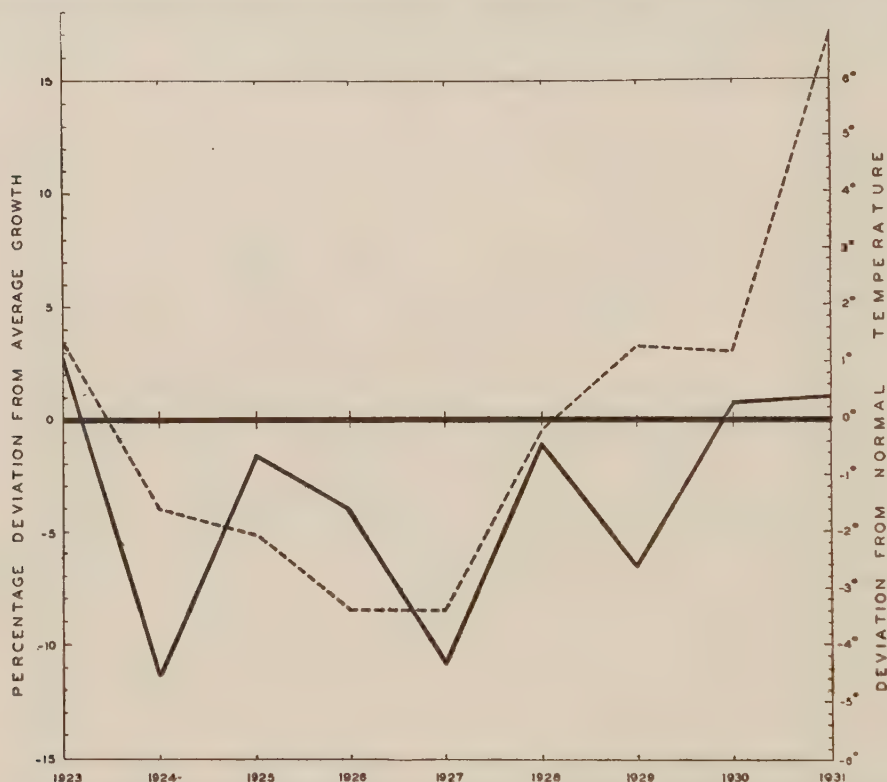


FIGURE 8.—Relationship in different calendar years between the deviation of growth of Clear Lake cisco from average and deviation of air temperature from normal during cisco's growing season. Deviation from average growth, broken line; deviation from temperature, solid line.

ness of growth for certain populations and over certain periods of years. For example, Trout, Silver, and Muskellunge Lakes agree in showing improvement in growth from 1928 to the relatively good year 1929, followed by a distinct drop to the relatively poor year of 1930. Similarly Trout, Muskellunge, and Clear Lakes agree in showing poor growth in 1926 and 1927.

Agreements of the sort just pointed out suggest that the amount of growth in different calendar years may possibly be determined in part by factors that affect all four lakes. The failure of any general agreement of the growth deviation curves indicates, however, that local conditions that exist within a single lake also exert a powerful influence on the amount of growth in different calendar years.

The most apparent influence that might affect growth similarly in all lakes is the average temperature during the growing season, while growth within a single

lake might be expected to vary somewhat with annual fluctuations in the abundance of the population within that particular lake. References to the literature on the question of the change in growth rate that accompanies change in the density of population have been made previously (pp. 254-257). Some mention should be made of the much less numerous observations on the relationship between annual fluctuations in average temperature and annual fluctuations in growth, particularly as these observations have been made with reference to coregonids.²⁶

Huitfeldt-Kaas (1917) demonstrated a close correlation between first-year growth and average annual temperature in the lagesild or pollan (*Coregonus albula*) of Mjøsen and Storsjø. At the same time he recognized the possible effect on growth rate of changes in the density of population from one year to another.

In a later paper (Huitfeldt-Kaas, 1927) he was able to show a relationship between the amount of growth and summer temperature in the gwiniad (*Coregonus lavaretus*) and the pollan (*C. albula*). (He noted a similar situation in several tribes of the trout (*Salmo eriox*).)

Olofsson (1932) compared the growth of three species of *Coregonus* (*C. wartmanni borealis*, *C. wartmanni generosus*, and *C. lavaretus*) of Norrland in the warm summer of 1930 with that in the cold summer of 1931. In all three forms there was large growth in the warm summer and slow growth in the cold. Olofsson called attention particularly to the fact that occasionally growth during a cold season may be so small that the year ring formed on the scales might easily be overlooked. Some scales may even fail to form a distinct year band. The differences observed between growth of the years 1930 and 1931 were exhibited by fish of different sizes and ages.

Krogus (1933) found that the curve of the deviation from average growth in different calendar years for *Coregonus lavaretus* of Lake Baikal followed closely the corresponding curves for deviation from average annual temperature and average annual precipitation.

Van Oosten (1929) found no relation between annual fluctuations in the air temperatures during the growing season and the annual fluctuations in the first year's growth in the Saginaw Bay herring (*L. artedi*).

There are no records of water temperature available upon which to base a comparison of annual deviation from normal temperature during the growing season and annual deviation from average growth in the cisco populations of this study. It is possible, however, to make a comparison between annual deviation from average growth and annual deviation from normal air temperature²⁷ in the region. For this purpose the records of the meteorological stations at Big St. Germaine Dam and Rest Lake Dam were taken as representative for Trout, Muskellunge, and Silver Lakes, while the records of the Minocqua station were taken as representative for Clear Lake.²⁸

Since the lengths of the growing seasons (pp. 249-253) are not the same in the different lakes the annual deviations from normal summer temperature were calculated

²⁶ Although his work does not deal with the coregonids, mention should be made of Segerstrale's (1932, 1933) observations on the relationship between summer temperature and the growth of fishes in southern Finland. This work dealt with the perch (*Perca fluviatilis*) and several species of cyprinids. Segerstrale found that the amount of growth during the summer is a quantity highly sensitive to the average summer temperature.

²⁷ Climatological Data for the United States, U. S. Department of Agriculture, Weather Bureau, vols. X-XVIII, 1923-31.

²⁸ Muskellunge Lake lies about 3 kilometers east of Trout Lake, and Silver Lake lies about 1 kilometer off the southwest corner of Trout Lake. The St. Germaine weather station is about 13 kilometers southeast of Trout Lake while the Rest Lake station lies at an approximately equal distance to the northwest of Trout Lake. The town of Minocqua is about 6 kilometers due west of Clear Lake.

from different combinations of months. The St. Germaine and Rest Lake data were used to determine the annual deviation from normal temperature for the periods May to July and May to August, both inclusive. The former period of time may be taken to correspond approximately to the growing season of the Trout Lake cisco, and the latter to the growing seasons of the Silver Lake and Muskellunge Lake ciscoes. The annual deviation from normal temperature for the longer Clear Lake growing season (May to September, inclusive) were determined from the Minocqua station data. In these calculations of deviations from normal temperature, records for a single month were found to be occasionally lacking in the data for a station. For these few gaps in the data the corresponding records of the nearest neighboring station were substituted. This substitution is justifiable for the corresponding deviations from normal temperature at the different stations were almost always close to each other in value.

Table 56 shows the annual deviations from normal air temperatures as based on the different combinations of months and for the weather stations mentioned in the preceding paragraph. These data are presented graphically in figures 6 to 8 along with the corresponding curves of deviation from average growth. The examination of these curves shows that there is little evidence of a connection between annual deviation from average growth and annual deviation of the air temperature from the normal during the growing season. In the Trout Lake data (fig. 6) the years (1924, 1928, and 1929) with better than average growth were years with subnormal temperature for the period, May to July. On the other hand, 1930 with a temperature slightly above normal was a poor growth year. The year 1929 was a good growth year in both Muskellunge Lake and Silver Lake (fig. 7), while 1930 was a year of poor growth. Yet the air temperature for the period, May to August, was below normal in 1929 and above normal in 1930. Certain other years, however, show both subnormal temperature and growth below average (for example, Silver Lake, 1924). There is some indication that in Clear Lake (fig. 8) there may be some slight connection between annual variations in growth and annual variations in average air temperature over the period May to September. It may be seen that in Clear Lake all the calendar years with poorer than average growth (1924 to 1928, inclusive) showed subnormal temperatures during the growing season while 3 of the 4 years with better than average growth (1923, 1929, 1930, 1931) had temperatures above normal during the growing season. The year 1929 showed growth slightly above average, but temperature below normal. In general, however, the Clear Lake curves for annual deviation of the cisco's growth from the average and the annual deviation of the air temperature during the growing season from normal show a rather conspicuous lack of parallelism.

TABLE 56.—Average deviation of air temperatures from normal during the growing season of the cisco
[Deviations are in degrees Fahrenheit; 1.8° F.=1.0° C.]

Stations	Months	1923	1924	1925	1926	1927	1928	1929	1930	1931
St. Germain Rest Lake..	May, June, July.....	2.0	-5.8	-1.6	-1.2	-3.5	-0.7	-2.4	0.2	-0.2
Do.....	May, June, July, August.	.8	-4.8	-0.2	-0.7	-3.6	-0.5	-1.9	.8	-0.6
Minocqua.....	May, June, July, August, September.	1.1	-4.5	-0.6	-1.6	-4.3	-0.4	-2.6	.8	.4

The failure of the data discussed in the preceding paragraph to show any clear dependence of growth in different calendar years on the temperature of the air during

the growing season should not be taken to show that in these four cisco populations the amount of growth in a particular summer does not depend in part on the temperature of the lakes' waters during the growing seasons of the several stocks. It must be recognized first that fluctuations in air temperature may not offer a perfect index of fluctuations in water temperature. A more probable explanation of the failure of annual fluctuations in temperature and in growth to show correspondence is that annual differences in growth are so closely dependent on some other factor or factors that the effect of annual differences in temperature are almost completely obscured. There is reason to believe that in the populations of this investigation the annual fluctuations in the goodness of growth may show some dependence on annual fluctuations in the densities of the different populations.

It has been shown previously (p. 262) that the growth rates (in weight) of these four populations follow the inverse order of the relative densities of their populations. In view of this demonstrated relationship between growth rate and density of population it might well be expected that within a single population changes in the density of the cisco may be accompanied by changes in its growth rate.

In the study of the age composition of the cisco samples from Trout Lake (table 45, p. 264) it was pointed out that the years 1926 and 1927 saw the production of abundant year classes, and that as the result of the abundance of these two groups the 1930 Trout Lake cisco samples were on the average composed of older fish than the 1928 samples while the 1931 samples were composed of older fish than either the 1928 or 1930 collections. This accumulation of old fish together with the contributions of young in the years later than 1927 probably caused the density of the population to be rather high in 1930. This increase in the density of the population may account in part for the drop in growth from 1929 to 1930.

The data for the Muskellunge Lake cisco also afford evidence for a dependence of growth variations on variations in population density. While the 1928 and 1930 collections contained only a few individuals more than 2 years old, a large number of the 1928 year class individuals were present as the III group in 1931. (See p. 264.) The great abundance of the III group in 1931 suggests that an accumulation of the stock may have been occurring in Muskellunge Lake in 1929 and 1930. This accumulation may possibly account for the drop in the amount of growth from 1929 to 1930.

The age and year class composition data for the Silver Lake cisco (table 47, p. 265) show that here as in Trout Lake there was probably an accumulation of the stock in 1930. In the examination of the data of table 47 it should be remembered that the large number of 1931 I-group fish causes the representation of the older age groups of the 1931 samples to appear relatively too low; the gear used in 1928 and 1930 captured few I-group individuals. If due consideration is given to the absence of the I-group fish in the 1928 and 1930 collections the relative abundance of the older age groups in the 1931 Silver Lake collections must be recognized to be higher than in 1930, while the 1930 collection in turn shows a greater abundance of old fish than the 1928 collection. In Silver Lake as in Trout Lake and Muskellunge Lake the accumulation of older fish was accompanied by a decrease in growth from 1929 to 1930.

It should be mentioned that the data upon which a suggested explanation of the drop in growth from 1929 to 1930 in Trout, Silver, and Muskellunge Lakes was based fail to offer any logical explanation for the improvement of growth from 1928

to 1929. Unfortunately there are no 1929 collections upon which to base a comparison of the age composition of that year with the years 1928, 1930, and 1931.

In the Clear Lake cisco the evidence for a dependence of annual fluctuations in the amount of growth on annual fluctuations in the density of the population is somewhat stronger than in the Trout, Muskellunge, and Silver Lake populations. The years 1923, 1924, and 1925 (p. 265, table 48, fig. 5) were undoubtedly excellent years for the production of young. The presence of three successive good hatches must have led to a considerable accumulation of the cisco stock. Corresponding with this accumulation the amount of growth per year decreased from 1923 to 1927 (fig. 8). The production of young was poor in 1926 and 1927. The occurrence of 2 poor production years combined with natural mortality could be expected to lessen the crowding of the population. The growth improved from 1927 to 1929, fell back a little in 1930, and improved again in 1931.²⁹

The relationship indicated in the Trout Lake, Muskellunge Lake, Silver Lake ciscoes, and especially in the Clear Lake cisco, between annual fluctuations in population density and annual fluctuations in growth is in agreement with Järvi's observations (1920, 1924) on the kleine Maräne (*Coregonus albula*).

The failure of variations in the amount of growth in different calendar years to show any close general dependence on either annual variations in temperature or annual variations in population density suggests that possibly these variations in growth depend closely on both factors, and that the failure of these factors to operate in the same direction in the same year tends to obscure the effect of each of them.

BIMODALITY IN THE CALCULATED GROWTH FOR THE FIRST YEAR OF LIFE

The examination of the frequency distributions of the calculated growth for the first year of life in the best represented age groups (tables 57 to 60) shows that some of these distributions have a distinct bimodality, which appears to be characteristic for a year class and present regardless of the age of the fish upon which the calculated growths were based.

TABLE 57.—Trout Lake cisco—Frequency distribution by 5-millimeter intervals of the calculated growth in length during the first year of life

Length	Year class							
	1926			1927		1928		1929
	II	IV	V	III	IV	II	III	II
	1928	1930	1931	1930	1931	1930	1931	1931
110.....	1				1	1		
105.....	1			1	1	1	1	1
100.....	4	1	1	7	4	5	6	2
95.....	6	2		14	4	8	15	6
90.....	7	8	5	17	16	6	34	13
85.....	9	21	15	32	24	7	31	20
80.....	15	30	23	74	48	5	26	12
75.....	30	20	27	85	78	3	31	6
70.....	26	11	6	83	72		26	1
65.....	3	6	2	30	18		3	
60.....				5	3			
55.....				1				

²⁹ The good growth in 1931 may have been in part due to the climatic conditions of that year as well as to the reduced number of ciscoes in the stock. The temperature over the period, May to September, inclusive, was only slightly above normal (table 56) but the autumn temperatures were exceptionally high (p. 253). It is probable that the warm autumn of 1931 gave the Clear Lake cisco a longer growing season in that year than it usually enjoys.

TABLE 58.—*Muskellunge Lake cisco*—Frequency distribution by 5-millimeter intervals of the calculated growth in length during the first year of life

Length	Year class				Length	Year class			
	1926	1928		1929		1926	1928		1929
	II	II	III	II		II	II	III	II
	1928	1930	1931	1931		1928	1930	1931	1931
125.....	2		2		90.....	20	39	28	56
120.....	6	2	7		85.....	35	41	64	22
115.....	28	8	16	3	80.....	29	26	60	4
110.....	24	20	46	7	75.....	17	12	17	1
105.....	35	21	39	33	70.....	1	2	5	
100.....	27	17	37	60	65.....	2			
95.....	16	21	26	72					

TABLE 59.—*Silver Lake cisco*—Frequency distribution by 5-millimeter intervals of the calculated growth in length during the first year of life

Length	Year class							
	1924	1925			1926		1927	1928
	IV	III	V	VI	IV	V	IV	III
	1928	1928	1930	1931	1930	1931	1931	1931
120.....								
115.....								
110.....								
105.....							1	2
100.....							4	5
95.....							8	4
90.....					1	2	5	4
85.....	5		1		1	7	8	7
80.....	8		3	3	9	11	8	9
75.....	17	6	2	4	10	36	20	9
70.....	22	11	9	7	16	29	21	16
65.....	12	17	2	4	11	16	26	9
60.....	3	7	6	1	7	6	5	3
55.....	2	5	2	1	2	1	4	2
					1			

TABLE 60.—*Clear Lake cisco*—Frequency distribution by 5-millimeter intervals of the calculated growth in length during the first year of life

Length	Year class									
	1924		1925		1928		1929		1930	
	VII	VIII	VI	VII	III	IV	II	III	I	I
	1931	1932	1931	1932	1931	1932	1931	1932	1931	1932
140.....								1		
135.....									2	3
130.....		1			1			1	3	1
125.....	2						1	1	5	
120.....	3	1		2	1	1	4	3	7	3
115.....	1	2	1	1	5	3	11	4	13	5
110.....	8	1	5	2	10	5	11	8	6	9
105.....	6	3	8	6	11	3	24	10	4	7
100.....	9	1	7	7	12	4	12	8		1
95.....	3	4	1	2	7	4	7	7		1
90.....		1	1	1	5	2	1	1		
85.....		1				3				

This bimodality of the length frequencies of the calculated growth for the first year of life may be found in the 1928 year class from Trout Lake and in the 1926 and 1928 year classes from Muskellunge Lake. All the other year classes from these two lakes, and all year classes from Silver Lake and Clear Lake, where the samples are large enough to give reliable results show unimodal distributions for the calculated growth of the first year of life. The fact that bimodality in the first year's growth occurs only in two populations and in only one or two year classes of these populations suggests that the occurrence of the phenomenon depends on the nature of the local conditions within each lake and that these conditions vary from year to year.

The most reasonable explanation for bimodality in the first year's growth lies in the assumption that in certain years there are two hatchings rather than a single one. In early spring a period of warm weather with brilliant sunshine and no strong winds can warm the waters of the shallow littoral region to a temperature several degrees above that of the main body of the lake. At such a time the development of the eggs of the cisco would be accelerated and some might hatch. If, however, there occurred before the completion of hatching season a period of cold, windy weather the temperature of the water of the littoral region would undergo a sudden drop of several degrees.³⁰ The development of the unhatched eggs would be retarded, and their hatching might be delayed for several days or even weeks. Such a situation would explain the observed cases of bimodality in the amount of growth during the first year of life. Eggs that develop in more exposed regions of a lake or in a lake more swept by winds would be less affected by fluctuations in weather conditions.

GROWTH COMPENSATION

The phenomenon of "growth compensation"—the tendency for individuals that grow relatively slowly in the early years of life to grow relatively rapidly during the later years—has been observed by numerous investigators and in several species of fish. The only study of growth compensation in the cisco was made by Van Oosten (1929) on the Saginaw Bay herring of Lake Huron. He concluded that "the large fish of an age group were the large fish in each preceding year of life * * * but that the differences between the small and large yearlings diminished each year of age—that is, the small yearlings were rapid growers and the large yearlings slow growers." Thus he found that compensation did occur, but that it was not sufficient to overcome completely any advantage in length which a large individual might hold at the end of the first year of life.

A comparison of growth compensation in age groups with unimodal and bimodal length distributions at the end of the first year of life should yield information as to the effect of the dispersion of the length frequency in early life upon the manner of growth in later life. In the 1931 collection from Muskellunge Lake (table 58) the distribution of the calculated lengths at the end of the first year is unimodal in the II group and bimodal in the III group. Both age groups are represented by large samples (258 for the II group and 347 for the III group). For these reasons they were selected as the basis for a study of growth compensation.

Table 58 shows the frequency distributions of the calculated lengths for both age groups at the end of the first year of life. The calculated length distributions of the

³⁰ Forel (1892) pointed out that the development of high temperatures in the littoral region depends on days of great calm and brilliant sunshine, and that this warming process proceeds slowly. The negative changes in temperature proceed much more rapidly. Forel observed that with a strong south wind the temperature of the littoral waters at the port of Geneva at times dropped as much as 6° C. to 8° C. or more from one day to another.

same groups at the end of the second year of life appear in table 61. Table 62 shows the frequency distribution of the increments of growth during the second year of life. All of these data are presented graphically as percentage frequencies in figure 9.

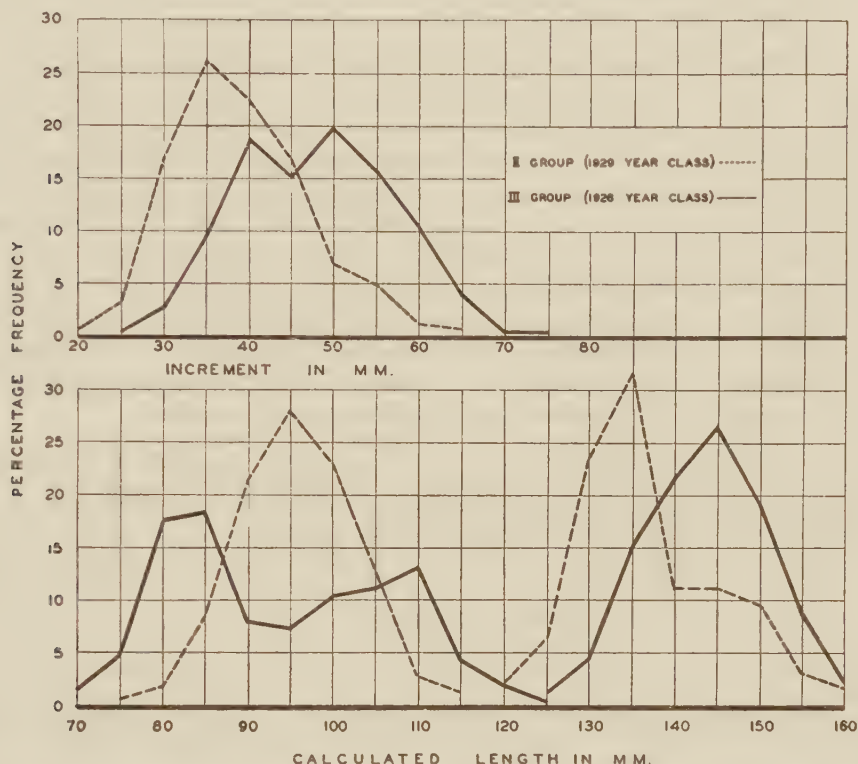


FIGURE 9.—Percentage frequency distribution of the 1931 samples of 1928 and 1929 year classes of Muskellunge Lake cisco with respect to calculated lengths at end of first year of life (below at left), the calculated lengths at end of second year of life (below at right), and calculated increments of growth during second year of life (above).

TABLE 61.—Muskellunge Lake cisco, 1931—Frequency distribution by 5-millimeter intervals of the calculated length at the end of the second year of life as based on the II group and the III group

Age group	Length interval									Total number
	120-124	125-129	130-134	135-139	140-144	145-149	150-154	155-159	160-164	
II.....	5	16	61	82	28	29	25	8	4	258
III.....		4	16	53	76	92	67	31	8	347

TABLE 62.—Muskellunge Lake cisco, 1931—Frequency distribution by 5-millimeter intervals of the calculated growth during the second year of life as based on the II group and the III group

Age group	Length interval												Total number
	20-24	25-29	30-34	35-39	40-44	45-49	50-54	55-59	60-64	65-69	70-74	75-79	
II.....	1	8	44	68	58	44	18	13	3	1			258
III.....		1	16	35	65	53	69	55	37	14	1	1	347

Examination of the data shows that during the second year of life of the III-group fish there occurred sufficient growth compensation to change the length distribution of the group from the bimodal to the unimodal condition. The existence of intense compensatory growth is indicated in the bimodal character of the curve for the second-year growth increments of the III group.

A more adequate conception is given of the growth compensation in these two age groups by the study of the correlations between the lengths attained at different times in the individual life histories, and the amounts of growth made by the individuals during different years of life. The correlation was computed for each age group for the following combinations of characters: (1) Calculated length at the end of the first year of life and calculated length at the end of the second year of life; (2) calculated growth in length during the first year of life and calculated increment of growth in length during the second year of life; (3) calculated length at the end of the first year of life and actual length at the time of capture. The results of these computations are given in table 63. Here L_1 is the calculated length at the end of the first year; L_2 is the calculated length at the end of the second year; ΔL_1 is the calculated growth during the second year; and L_T is the actual measured length at the time of capture.

TABLE 63.—*Muskellunge Lake cisco, II and III groups of 1931—Correlations between calculated length at the end of the first year and calculated length at the end of the second year, between the amount of growth during the first year and during the second year, and between the calculated length at the end of the first year and total length at the time of capture*

Data upon which the correlation is based	Coefficient of correlation and its probable error	
	II	III
L_1 and L_2	0.513±.046	0.708±.027
L_1 and ΔL_1	-.0.311±.056	-.0.828±.017
L_1 and L_T	.404±.052	.399±.045

Tables 64 to 67 show the data from which the correlations between L_1 and L_2 and between L_1 and ΔL_1 were calculated. The examination of tables 64 and 65 shows clearly that in both the II group and the III group the smaller fish at the end of the first year of life tend to be the smaller fish at the end of the second year of life, and that this tendency is the greater in the III group. Tables 66 and 67 show that in both age groups the individuals that grew least in the first year of life tend to grow most in the second, and that here again the tendency is more pronounced in the III group than in the II group.

TABLE 64.—*Relationship between calculated length in millimeters at the end of the first and second years of life in the Muskellunge Lake cisco, II group of 1931*

Calculated length at end of second year of life	Calculated length at end of first year of life									Total
	75-79	80-84	85-89	90-94	95-99	100-104	105-109	110-114	115-119	
160 to 164.....							2	2		4
155 to 159.....					1	2		2	3	8
150 to 154.....			1	2	4	7	10			25
145 to 149.....			3	7	13	7	8			29
140 to 144.....		1	2	2	13	6	3	3		28
135 to 139.....			4	15	28	28	7			82
130 to 134.....		3	7	22	16	10	3			61
125 to 129.....	1		4	6	5					16
120 to 124.....			3	2						5
Total.....	1	4	22	56	72	60	33	7	3	258

TABLE 65.—*Relationship between calculated length in millimeters at the end of the first and second years of life in the Muskellunge Lake cisco, III group of 1931*

Calculated length at end of second year of life	Calculated length at end of first year of life												Total
	70-74	75-79	80-84	85-89	90-94	95-99	100-104	105-109	110-114	115-119	120-124	125-129	
160 to 164								1	1	2	3	1	8
155 to 159				1			4	5	10	8	2	1	31
150 to 154			2	4	5	5	9	16	20	4	2		67
145 to 149	1	3	11	18	14	7	12	11	13	2			92
140 to 144		1	20	22	6	10	10	5	2				76
135 to 139	1	8	19	15	3	4	2	1					53
130 to 134	2	4	6	4									16
125 to 129	1	1	2										4
Total	5	17	60	64	28	26	37	39	46	16	7	2	347

TABLE 66.—*Relationship between amount of growth in millimeters during the first year of life and the amount of growth during the second year of life in the Muskellunge Lake cisco, II group of 1931*

Calculated growth during second year of life	Calculated growth during first year of life									Total
	75-79	80-84	85-89	90-94	95-99	100-104	105-109	110-114	115-119	
65 to 69			1							1
60 to 64			1	2						3
55 to 59		1	2	4	4	2				13
50 to 54	1	2	1	5	3	3	2	1		18
45 to 49		1	7	9	9	9	6	3		44
40 to 44			6	17	18	5	10		2	58
35 to 39			4	15	27	17	4		1	68
30 to 34				3	8	23	7	3		44
25 to 29				1	3	1	3			8
20 to 24							1			1
Total	1	4	22	56	72	60	33	7	3	258

TABLE 67.—*Relationship between amount of growth in millimeters during first year of life and amount of growth during the second year of life in the Muskellunge Lake cisco, III group of 1931*

Calculated growth during second year of life	Calculated growth during first year of life												Total
	70-74	75-79	80-84	85-89	90-94	95-99	100-104	105-109	110-114	115-119	120-124	125-129	
75 to 79	1												1
70 to 74		1											1
65 to 69	1	3	6	4									14
60 to 64	2	5	19	9	2								37
55 to 59	1	4	17	23	8	1		1					55
50 to 54		3	15	20	14	7	8	1	1				69
45 to 49		1	2	7	2	10	10	12	8	1			53
40 to 44			1	1	2	8	16	14	17	5	1		65
35 to 39							3	9	15	5	2	1	35
30 to 34								1	5	5	4	1	16
25 to 29								1					1
Total.....	5	17	60	64	28	26	37	39	46	16	7	2	347

On the basis of the data that have been presented it is possible to draw the following conclusions concerning growth compensation as it is indicated in the two age groups considered here:

(1) Growth compensation occurs in both the group with a unimodal distribution of calculated lengths at the end of the first year of life and the group with a bimodal distribution of these lengths (negative correlation of L_1 and ΔL_1).

(2) Growth compensation is more intense in the group with the greater dispersion of the calculated lengths at the end of the first year of life (higher negative correlation between L_1 and ΔL_1 in the III group). The tendency toward compensation can lead to a bimodal distribution of the growth increments for the second

year, and can within a single season change the length distribution of the group from a bimodal to a unimodal condition.

(3) When the length distribution at the end of the first year of life is unimodal and the dispersion small, individual length at the end of the first year of life exerts more effect on individual length at the end of the second year of life, than the amount of growth during the first year of life exerts on the amount of growth during the second year of life. (In the II group the positive correlation of L_1 and L_2 is greater than the negative correlation between L_1 and ΔL_1 .) In the group with the greater dispersion and the bimodal distribution of lengths at the end of the first year of life the situation is reversed, that is, there is a closer connection between the amount of growth during the first year of life and the amount of growth during the second year of life than there exists between the length at the end of the first year and the length at the end of the second year. (In the III group the negative correlation between L_1 and ΔL_1 is greater than the positive correlation between L_1 and L_2 .)

(4) In spite of the growth compensation that occurs there is a tendency for the individual to hold throughout life a part of any advantage in length which it may hold at the end of the first year of existence. Compensation reduces individual advantage in length, but does not obliterate it (positive correlation in both groups between L_1 and L_T).

GROWTH RELATIONSHIPS IN THE TROUT LAKE, MUSKELLUNGE LAKE, SILVER LAKE, AND CLEAR LAKE CISCO POPULATIONS

Throughout the preceding sections attention has been called repeatedly to the order in which the cisco populations of the four lakes arrange themselves with respect to certain characteristics such as growth rate, sex ratio, condition, and the like. In view of the apparent high degree of correspondence among certain of these orders of arrangement it is considered advisable to present the data concerning them in a summarized form, together with a brief discussion and review of the possible significance of the observed correlations. Table 68 shows that arrangement of the lakes with respect to the amount of bound carbon dioxide in their waters and to the amount of organic matter in the plankton, and also with respect to certain phases of the life history of the cisco. Although these data demonstrate a close dependence of certain phases in the life history of the cisco on the conditions of its animate and inanimate environment, as will appear in the following discussion, any attempt to describe these relationships in precise terms of cause and effect meets with serious difficulty.

TABLE 68.—Order of the 4 lakes with respect to the concentration of bound CO_2 and the abundance of organic matter in the surface plankton, and also with respect to certain phases of the life history of the cisco

Item	Lakes			
	Clear	Muskellunge	Silver	Trout
Growth in length.....	1	2	3	4
Growth in weight.....	1	3	2	4
Bound CO_2 in water.....	4	3	2	1
Density of population.....	4	2	3	1
Length of growing season.....	1	3	2	4
Sex ratio (females per 100 males).....	4	2	3	1
Organic matter in plankton.....	4	1	3	2
Condition (K).....	1	4	2	3
Average length of life.....	1	4	2	3

Before entering into the discussion of the relationship between growth rate and the environmental factors that may affect it, attention should be called to the fact that the order of the four lakes with respect to growth in length is not the same as their order with respect to growth in weight. Although the Muskellunge Lake cisco shows better growth in length than the Silver Lake cisco, its growth in weight is inferior to that of the Silver Lake population. The reason for this reversal of order lies in the very poor condition of the Muskellunge Lake fish. Weight unquestionably furnishes a better measure of increase in living matter than does length, but for the purposes of the present discussion it will probably be sufficient to consider both populations merely as intermediate between the extreme conditions represented by the Trout Lake cisco and the Clear Lake cisco.

PHYSICAL-CHEMICAL FACTORS

Certain factors may be ruled out immediately as inadequate for the observed differences in the growth rates of the four populations.

Temperature fails to account for the observed differences in growth rate. Since all four lakes are located within a short distance of each other the climatic conditions that affect each of them are essentially the same. Differences in the size and form of the various basins may lead to differences in average water temperature during the summer, but here it should be pointed out that while the cisco finds its coldest summer habitat in Trout Lake and Clear Lake, the populations of these two lakes represent the extremes in growth rate.

Oxygen conditions also fail to explain the differences in the growth rates of the four populations. Here, as was the case with temperature, Trout Lake and Clear Lake resemble each other most closely. Each possesses large masses of well oxygenated water in the hypolimnion, the favorite habitat of the cisco.

The abundance of bound CO_2 and the closely related hydrogen-ion concentration and conductivity are the only physical-chemical characteristics known to show any correlation with growth rate. Growth rate in length and the abundance of bound carbon dioxide stand in an inverse relationship to each other. It is hardly reasonable to assume that an abundance of bound CO_2 impedes growth directly or that a scarcity of bound CO_2 accelerates it. The effect of the abundance of CO_2 on growth rate is probably indirect and operative through its modification of the biological nature of the cisco's environment.

In general, the amount of bound CO_2 in a lake's waters is roughly indicative of the biological productive capacity of that lake. In view of this fact it would hardly be expected that the poorest growth of the cisco would occur in the lake with the greatest concentration of bound CO_2 . This apparently paradoxical situation is explained, however, if it is assumed that an abundance of bound CO_2 makes not only for a greater production of food organisms, but also makes for a much greater abundance of the ciscoes themselves, and that the abundance of the ciscoes in turn determines their growth rates. Such an assumption has the support of the observed fact that the cisco population is most dense in Trout Lake with the greatest amount of bound CO_2 , and sparsest in Clear Lake with the least amount of bound CO_2 , while Muskellunge Lake and Silver Lake with intermediate concentration of bound CO_2 have populations of intermediate densities.

DENSITY OF POPULATION

The section on the relationship between density of population and growth rate inclined toward the opinion that differences in the severity of competition for food related to differences in the densities of the various populations are largely responsible for differences in the growth rates of the four cisco stocks. This opinion was presented as the most logical, even in the face of the facts, first that the actual existence of any competition for food in any one of the four populations remains to be demonstrated, and second that there exists a strong possibility that crowding may impede growth independently of competition for food (Willer's "Raumfaktor").

As to the causes of the observed differences in the densities of the four populations it may be seen, as was mentioned previously, that the greatest density of the cisco population occurs in the lake with the heaviest concentration of bound CO_2 (Trout Lake) while the least density occurs in the lake with the lightest concentration of bound CO_2 (Clear Lake). The positions of Silver Lake and Muskellunge Lake are reversed with respect to the concentration of bound CO_2 and the density of population, but both are intermediate to the conditions found in Trout Lake and Clear Lake.

Since it is generally held that the success or failure of a hatching of fish depends primarily on conditions that determine the survival of the young at a very early stage, it does not appear unreasonable to hold that differences, traceable to the concentration of bound CO_2 , in the amount and kind of plankton available to newly hatched ciscoes may account for the observed differences in the densities of the four populations. A study of the plankton cycle in each lake should throw light on the subject.

There does not appear to be any complete correlation between the amount of organic matter in surface samples of plankton taken during the summer and the density of the cisco populations. Although Clear Lake with the least amount of organic matter in the surface plankton has the sparsest cisco population, Trout Lake, with the densest cisco population does not have the greatest amount of organic matter in the surface plankton.

It is possible further that these differences in the densities of the cisco populations may depend on yet other factors such as the availability of suitable spawning areas or the destruction of eggs and young by predators.

Regardless of whether it is held that differences in growth rate depend directly on differences in population density or that both are dependent on yet other factors, it must be admitted that growth rate and density of population show a very close correlation.

LENGTH OF THE GROWING SEASON

In the general section under this title it was pointed out that differences in the growth rates of the four cisco populations can be explained in part by actual differences in the length of the cisco's growing season in the various lakes. The Trout Lake cisco has definitely the shortest growing season, followed by the Muskellunge Lake cisco, the Silver Lake cisco, and the Clear Lake cisco in the order named. Thus it may be seen that in the four populations the length of the growing season follows the same order as their growth rates (in weight) and the inverse order of their densities of population.

These differences in the length of the growing season cannot be accounted for on the basis of temperature and oxygen conditions for the same reasons that temperature and oxygen conditions fail to account for the differences in growth rate. (See p. 287.)

It is possible that an explanation of the differences in the lengths of the growing season may be found in the study of the plankton cycles in the four lakes. Particular attention should be given to the abundance at all times of the season, and in the strata actually inhabited by the cisco, of the plankton forms most commonly taken by that species.

A second possible explanation of the differences in the length of the cisco's growing season in the various lakes is suggested by the fact that in fishes in general the termination of the season's growth in adult fish is coincident with the onset of the development of the gonads preliminary to spawning. (The determination of the length of the growing season in the four cisco populations was based almost entirely on mature and maturing individuals.) Since the average size (weight) of the spawning individuals of the four populations follows the same order as their growth rates and the lengths of their growing season, it is suggested that the development of the gonads in small spawners may begin earlier in the season than in large spawners, and that the slowness of growth of a slow-growing population may be thereby accentuated.

PARASITIZATION

The only published data on the incidence and severity of parasitization in the cisco populations of Trout, Muskellunge, Silver, and Clear Lakes are those presented by Dr. Chancey Juday in the Bureau of Fisheries' report on Progress in Biological Inquiries 1931 (Higgins, 1932). Juday summarized the data then available as follows:

Thirty ciscoes from Silver Lake were examined for parasites, and cestodes were found in the intestines of all of them; 80 percent of them also had *Acanthocephala*. In Muskellunge Lake 80 percent of the ciscoes contained cestodes and 20 percent were free of visceral parasites. In Trout Lake 16 percent were negative, 82 percent had cestodes in their intestines, and 10 percent also had *Acanthocephala*. The ciscoes from Clear Lake, on the other hand, were 96 percent negative; only 2 specimens out of 60 examined yielded any parasites. These fish were found to be feeding almost exclusively on *Daphnia*, and this may be partly responsible for the very small parasite infestation. Clear Lake also has very soft water, and the snail population, as a result, is relatively small, so that the danger of parasite infestation from this source is correspondingly small.

Although the above data show that the Clear Lake cisco with the fastest growth rate has the lightest parasite infestation, the relationship between parasite infestation and growth rate in the remaining three populations is not clear. The solution of the problem concerning the relationship between growth rate and parasite infestation in the cisco awaits the examination, within each population, of the effect of individual parasitization on individual growth rate.

CONDITION

In the section that dealt with condition and the relationship between length and weight it was pointed out that the order of the four lakes with respect to the average condition of their cisco populations, from poorest to best, is: Muskellunge, Trout, Silver, Clear. While this arrangement does describe the order of the lakes with respect to condition as based on the samples taken, it is open to the criticism that because of the variation of K with length, additional samples taken in yet other years and showing different length distributions of the fish might possibly bring about a change in the arrangement. The determination of an average value of K within a population depends, first, on the manner of change of K with length and, second, on the length distribution of the fish used.

It is quite possible that the most significant phase of the study of condition in these four cisco populations does not lie in the determination of average values of K for the different stocks but lies rather in the study of the change of condition with increasing length. This is particularly true since the separation of the lakes with respect to the manner of change of K with increased length is much sharper than it is with respect to the average value of K in the entire population. The significance of the changes of K with length will become more apparent with the examination of

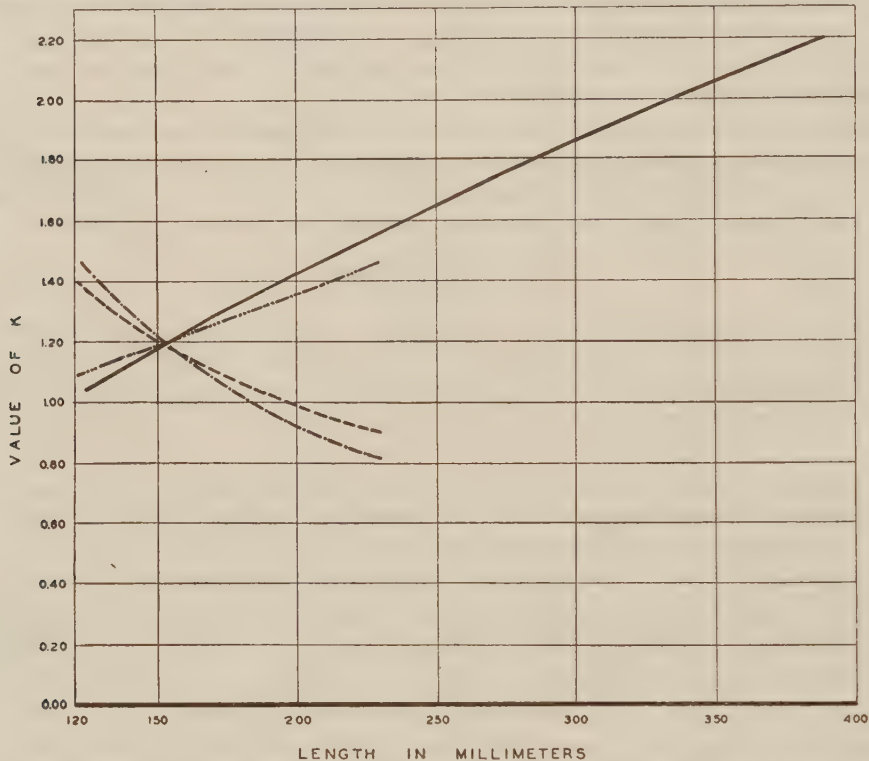


FIGURE 10.—Theoretical values (in 1931) of the coefficient of condition (K) at different lengths, calculated from equations of the type $K=C \times 10^6 L^m$. Trout Lake, ---; Muskellunge Lake, -.-.; Silver Lake (females), -...-; Clear Lake (females), ...

the equations that describe K as functions of length. These equations for 1931 (the only year in which samples were taken from all four lakes) are: ³¹

Muskellunge Lake:

$$K=141.924 L^{-0.04932}$$

Trout Lake:

$$K=38.7640 L^{-0.69245}$$

Silver Lake (females):

$$K=0.12322 L^{0.46372}$$

Clear Lake (females):

$$K=0.04555 L^{0.64091}$$

The theoretical values of K at different lengths, calculated from the above equations appear in table 69 and are presented graphically in figure 10.

³¹ For the purposes of this discussion one equation from each lake is sufficient. The equations for the males of Silver and Clear Lakes may be found in table 27.

TABLE 69.—*Theoretical values of the coefficient of condition (K) at different body lengths, calculated from equations based on 1931 collections*

Lake	Length in millimeters																		
	130	140	150	160	170	180	190	200	210	220	230	250	270	290	310	330	350	370	390
Trout.....	1.332	1.266	1.207	1.154	1.107	1.064	1.025	0.989	0.956	0.926	0.898	-----	-----	-----	-----	-----	-----	-----	-----
Muskellunge.....	1.397	1.302	1.220	1.147	1.083	1.026	.975	.928	.886	.848	.813	-----	-----	-----	-----	-----	-----	-----	-----
Silver (females).....	1.122	1.160	1.197	1.232	1.267	1.300	1.332	1.357	1.394	1.424	1.453	-----	-----	-----	-----	-----	-----	-----	-----
Clear (females).....	1.077	1.131	1.182	1.233	1.283	1.331	1.379	1.426	1.471	1.517	1.561	1.648	1.733	1.815	1.895	1.974	2.051	2.126	2.200

The remarks, made previously (p. 246), concerning the validity of using length-weight equations for the calculation of unknown lengths or weights outside the range of the empirical data apply likewise to the calculation of unknown values of K for lengths outside the range of empirical data. However, it may be pointed out further, on purely mathematical grounds, that the K equations cannot possibly be used for the calculation of K values in very small fish, since as length approaches zero the values of K increase without limit in the equations with negative exponents and approach zero in the equations with positive exponents.

In the 1931 K equations it may be seen that the order of the four populations with respect to the value of the exponent, m , which describes the rate of change of K with change of length, is: Muskellunge Lake, Trout Lake, Silver Lake, Clear Lake. The differences in these rates of change are reflected in the forms of the curves of figure 10. Here it may be seen that the Muskellunge Lake cisco loses condition rapidly with increase in length. The Trout Lake cisco also loses condition with increase in length, but at a slower rate than does the Muskellunge Lake cisco. In Silver Lake the condition of the cisco improves with increase in length, although this improvement is not as rapid as it is in the Clear Lake cisco. The courses of the curves indicate further that at a length of between 150 and 160 millimeters the conditions of all four populations are closely similar.

If the above facts are examined in relation to the growth rates of the four populations it may be seen that, while the Clear Lake cisco with the most rapid growth shows the most rapid progressive improvement in condition, the Trout Lake cisco with the least rapid growth does not show the most rapid loss of condition. Although the Muskellunge Lake cisco shows better growth than the Trout Lake cisco with respect to both length and weight, the loss of condition with increase in length proceeds considerably more rapidly in the former population. This fact demonstrates at least a partial independence between the factors that determine growth rate and the factors that determine condition. Further, the fact that the factors which bring about a rapid loss of condition in one population may fail to reduce the growth rate of this population below that of a second stock with a less rapid loss of condition may be construed as a strong argument for the operation of the "space factor" in the determination of growth rate.

The data of table 68 show that the arrangement of the four lakes with respect to average condition and the rate of change of condition follows the reverse order of their arrangement with respect to the average abundance of the organic matter in the surface samples of plankton. (The greater number of these plankton samples were taken during the summer months.) Although the abundance of organic matter in surface samples of plankton may not serve as a wholly reliable index of the abundance of plankton forms most commonly taken by the ciscoes and in the strata of

water inhabited by that species, the data do show that the cisco suffers the most rapid loss of condition with increase in length and shows the poorest average condition in the lake (Muskellunge) with the most eutrophic environment, while the most rapid gain in condition and the best average condition are found in Clear Lake with the most oligotrophic environment. While it is hardly to be inferred that a mere abundance of food causes loss of condition in the cisco or that a scarcity of food makes for better condition, it is quite probable that the cisco does not thrive in the physical and chemical conditions most conducive to a large production of food organisms. The eutrophic environment of Muskellunge Lake may, for example, force the cisco to live under such undesirable conditions of temperature and dissolved oxygen that it fails to thrive even in the presence of abundant food, while in Clear Lake favorable physical and chemical conditions may make it possible for the cisco to reach the best of condition on a substantially smaller basic abundance of food.

Average longevity and condition appear to be more closely correlated than average longevity and growth, for the four populations follow exactly the same order with respect to the two first-named characteristics. Such a relationship is logical. With particular reference to the populations whose K equations show negative exponents, it appears probable that the progressive loss of condition with increase in length may bring the cisco to a point of emaciation beyond which survival is impossible. Since length is a function of age the imposition of a limit on the length that can be attained places also a limit on age. It has been pointed out previously (p. 246) that in the Trout Lake cisco the few very old individuals taken had not followed the same length-weight relationship that held for the main body of the population.

The relationship between individual condition and individual parasite infestation is not known. The Clear Lake cisco with the lightest parasite infestation of any of the four populations is the population with the best condition.

SEX RATIO

The cisco population of the four lakes follow the same order with respect to growth in weight and the average relative abundance of males. In the section on sex ratio it was pointed out that the less viable males probably suffer greater mortality under adverse conditions that produce slow growth, and hence that the correlation between growth rate and sex ratio may be considered to result from the dependence of these two characteristics on the same environmental factors.

GENERAL REMARKS

The failure of certain of the growth relationships of the cisco to conform to generally accepted principles and theories suggests that, on the basis of our present knowledge, generalizations concerning these relationships are scarcely safe. A satisfactory understanding of the growth relationships of the cisco can be attained only after exhaustive studies into the biology of this form. Further, the great plasticity and adaptability of the cisco makes advisable the study of its biology in the greatest possible diversity of habitats.

An illustration of the dangers of making generalizations concerning the growth and biology of the cisco is offered by the examination of the relationship between

condition (*K*) and environmental factors. The data of this study indicate that the cisco is in the best condition in the most oligotrophic environment and in the poorest condition in the most eutrophic environment. However, the situation found in the Indian Village Lake (Indiana) shows that such a relationship cannot be considered general for this plastic species. Although the lakes of northeastern Indiana are of the extreme eutrophic type and the Indian Village Lake cisco lives under what are apparently the most undesirable conditions with respect to temperature and oxygen conditions (Scott, 1931), the Indian Village Lake cisco shows excellent growth and is in better condition than any but the Clear Lake population of this study (p. 249).

FISHES ASSOCIATED WITH THE CISCO

There is little resemblance among the fish associations of which the four cisco populations are parts. In table 70 are recorded the numbers of individuals of all species taken in the nets used for the cisco. Fish are considered to have been taken along with the cisco if they were taken in a net of any mesh set at the same time and approximately the same depth as the nets that caught ciscoes.

TABLE 70.—*Numbers of individuals of other species of fish taken in the net catches along with the cisco samples*

Species	Lakes			
	Trout	Muskellunge	Silver	Clear
Cisco.....	1, 197	1, 863	524	465
Perch.....		1, 543	1	5
Pike-perch.....				37
Rock bass.....		8		1
Sucker.....		130		
Lake trout.....	32			
Whitefish.....	32			
Burbot.....	1			
Smallmouth black bass.....		14		

In Trout Lake the fish taken with the cisco were all typical deep-water forms. There is no evidence that the deeper regions of the lake are invaded by individuals of the shallow-water forms. The trout were mostly large individuals that were caught and held by the teeth in small mesh nets.

The situation in Muskellunge Lake is unusual. The close association of the cisco with shallow-water forms is the result of the deficiency in oxygen that drives the ciscoes up from the lower, cooler strata of the lake.

In Silver Lake the cisco is practically isolated, at least during the late summer. The single perch taken at a depth of 14.5 meters may be considered a straggler.

In Clear Lake the pike-perch that were taken regularly along with ciscoes appear to be distributed generally throughout the region occupied by the cisco in this lake. The five perch were taken at depths between 19.5 and 24.5 meters. The rock bass was captured at a depth of 15.5 meters. Since both rock bass and perch are known to be plentiful in the shallow water of this lake their presence in the hypolimnion may be considered more or less as accidental.

In all the lakes the nature of the associations of which the ciscoes are part probably undergoes considerable change according to the time of year.

SELECTIVE ACTION OF GILL NETS

REVIEW OF PREVIOUS INVESTIGATIONS

Since the collections upon which the present investigation is based were made by means of gill nets, it is of importance to have some measure of the selective action of the nets used upon the various populations sampled. Several investigators have presented observations on the selective action of gill nets, and some of these observations have been made with specific reference to the problem of securing samples for the study of age, growth, and length distributions within a population.

Much of the published material on the selective action of gill nets has been included incidentally in growth and life history studies. Other data have been presented in routine fishery reports. Because of the generally scattered nature of these data on gill-net selectivity and because of the importance to fisheries biologists of having a more adequate idea of the reliability of the samples that they take with gill nets, the presentation of the data of this investigation on the question of gill-net selectivity will be preceded by a brief review of the literature ³² on the subject.

The problem presented by the selective action of gill nets in the collection of materials for scientific investigations has been known for several decades. The Report on the Sea and Inland Fisheries of Ireland for 1902 and 1903 ³³; Part II—Scientific Investigations, contained in the report of the scientific adviser the statement that the investigation of herring shoals met a great difficulty in the selective action of the nets used in the commercial fishery. It was stated further, however, that the results of fishing nets of different meshes together (these experiments were made in another connection) indicated "that the selection is much less in practice than it would seem to be in theory. * * *

Delsman (1914) in his study of the age and growth of the North Sea and Zuider Zee herrings presented data to show that the selective action of the gear used in obtaining samples can exert an important effect on the nature of the results obtained from the study of those samples. He compared samples of drift nets and of seines of different sizes of mesh. From his observations he concluded:

Fänge an derselben Stelle mit Netzen verschiedener Maschenweite gemacht, werden verschieden sein und die Zusammensetzung des Fanges nach Grösse und Alter wird von der Maschenweite abhängen. Fischt man dagegen mit demselben Netz an verschiedenen Stellen * * * so werden auch die Fänge verschieden sein, und die Verschiedenheiten in ihrer Zusammensetzung werden durch die Zusammensetzung der Heringsschwärme im Meer bedingt werden.

Bjerkan (1917) disagreed with Delsman as to the great importance of selectivity of gear in determining the nature of herring samples from drift nets. From the comparison of trawl and drift-net catches he concluded that selection through the failure of drift nets to take smaller fish "cannot be very material." He pointed out further that "drift caught samples may point to the presence of rich year classes of very different ages." As to the effect of mesh size on the composition of drift net catches he stated further that "the size of mesh in the nets used affects the composition of the catches, but not to such an extent as might have been expected."

Further data on the action of drift nets were presented by Borley and Russell (1922). In connection with the study of the herring trawl fishery they measured the

³² No claims are made as to the completeness of this review; it should, however, bring together a sufficient mass of the miscellaneous data on the subject to furnish a good general conception of the nature of the problem of gill-net selectivity.

³³ Published in 1905.

catches of herring in drift nets of three sizes of mesh.³⁴ They summarized their results as follows:

According to these samples the finer-meshed nets caught the larger fish. The conclusion to be drawn is that the size distribution of the drift-net catch is probably not determined to any great extent by the selective action of the net.

Buchanan-Wollaston (1927) included with his discussion of the selective action of a trawl net certain observations as to the method of selection in drift nets. He called attention to the fact that drift nets do not capture all fish in the same manner. He pointed out that certain large individuals are retained by the maxillary barbs; some small individuals are held only because of the gill covers; while the majority are held between the gill covers and the dorsal fin. The different types of net action may lead to discontinuity in the length distribution of the catch.

Hodgson (1927) presented the analysis of data from the catch of herrings in three drift nets of different-size mesh.³⁵ Although the number of specimens was not great his results showed clearly that selective net action can lead to erroneous conclusions concerning the size and age composition of a population and also lead to inaccurate determinations of average lengths for the various age groups. Later the same author (Hodgson, 1933) presented the results of further experiments on the selective action of drift nets. These experiments were conducted with particular reference to the effect on the herring stock of the size of mesh in the drift nets employed in the commercial fishery. On the basis of two separate experiments Hodgson concluded:

that there is a very definite and subtle gradation in the length of the herrings caught by nets of even slightly different meshes, and it is also plain that the whole character of a fishery can be changed by the use of different nets.

These investigations were all concerned with a single marine fishery—the drift-net fishery for herring. The opinions of the different investigators, however, show considerable disagreement.

Of greater interest with respect to the present study are the data concerning the selective action of gill nets as they are fished in fresh water. In the following paragraphs certain of the available data with respect to the selective action of gill nets are mentioned briefly. The various investigations are treated in general in the chronological order of their appearance without any attempt at grouping according to variety or kind of fish concerned.

Järvi (1920) compared the catches of the kleine Maräne (*Coregonus albula*) taken by seine with those taken by a series of seven nets having meshes ranging from 10 to 15 millimeters (bar measurement). The length compositions of the samples from the two sources agreed well.

Järnefelt (1921) noticed that his growth curves for several species of fish showed irregularities that could be traced to the selective action of the nets that he used in obtaining his samples. Concerning these irregularities Järnefelt stated: “* * * dass es ebenso viel Senkungen der Kurve gibt wie Netze verschiedener Maschenweite benutzt werden.” However, Segerstråle (1933) held that the irregularities observed by Järnefelt and others in growth curves resulted to a large extent from inaccurate methods of calculating growth from scale measurements, and that

³⁴ The sizes were 30, 31, and 33 meshes to the yard (bar measurement).

³⁵ The nets used had 35, 38, and 48 meshes to the yard (bar measurement).

irregularities in growth curves resulting from the selective action of nets are on the whole small.

Creaser (1926) in connection with his study of the growth of the sunfish (*Eupomotis gibbosus*) observed that gill nets are "particularly selective in their collecting" and advocated the use of a wide range of mesh size in gathering material for biological investigation, but included no data on the selective action of gill nets.

Koelz (1926) pointed out that in the Lake Ontario chub (*Leucichthys* spp.) fishery an increase of a quarter inch in the stretched measure of the mesh (from 2½ to 2¾ inches) reduced the number of fish taken by more than half.

Pritchard (1928) presented data on the selective action of six different sizes of mesh as that action affected the individual weight of Lake Ontario chubs (*Leucichthys* spp.). (The mesh size of his gill nets ranged from 1½ to 3 inches, stretched measure.) On the basis of his observations he stated, "The difference of one-quarter of an inch in the size of mesh may mean to the fishermen either a profitable or a 'starvation' industry." In a later paper (Pritchard, 1931) he presented the numbers of chubs of all species taken in nets of 12 different sizes of mesh (1¼ to 5 inches). Some data were included on the average lengths of the fish taken in different mesh nets. The data of Pritchard's 1931 paper agree with his earlier findings in indicating that a very small increase in the size of mesh may produce a great decrease in the number of fish taken.

Hart (1928) published detailed data on the length distribution of pike-perch and saugers of Lake Nipigon and Lake Abitibi taken in 6 different sizes of mesh ranging from 1½ to 4½ inches, stretched measure. Although Hart confined his discussion to the question of the proper legal mesh size in the commercial fishery, his data on the length distribution of the catches in different mesh size show clearly that a single size of mesh can take these spiny-rayed fish over a considerable length range. In a later paper (Hart, 1931) the same author pointed out that observed differences in the growth rate of the whitefish (*Coregonus clupeaformis*) in different parts of Lake Ontario could be explained in part by the tendency for the gill nets used in collecting samples from some localities to take only the larger fish of the younger age groups while pound-net samples were largely free from such selection. A more detailed consideration of the selective action of gill nets on whitefish appeared in Hart's (1932) study of the population statistics of Shakespeare Island Lake. (His experimental gear included 11 sizes of mesh, 1½ to 5 inches.) Hart found a correlation of 0.84 ± 0.01 between size of mesh and size of fish in Shakespeare Island Lake, while in Nipigon the correlation between the same variables was 0.51 ± 0.02 . He pointed out further that "large fish may be taken in small meshed nets although small fish are practically never taken in nets of coarse mesh."

Lechler (1929), referring to the selectivity of gill nets used in the fishery for the Reinanke (*Coregonus fera*) held that the selective action of the net is quite sharp. He stated: "Die Zusammensetzung der Fänge nach den Jahresklassen und damit die Grösse der Fische ist eine Funktion des Umfangs und direkt von der Netzmaschenweite abhängig." Further experiences caused him to modify this view slightly, for in a later publication (Lechler, 1930) he observed, "Die Fängigkeit der Netze ändert sich je nach der Beschaffenheit eines Bestandes."

Wright (1929) eliminated the younger age groups from his growth data on the rock bass (*Ambloplites rupestris*) as the selective action of the nets caused these early groups to have too high average values for length.

Haakh (1929) in his study of the age and growth of several species of fish in the Bodensee found that net selection led to inaccurate determinations of the average length of some age groups.

Wagler (1927, 1930a, 1930b, 1932, 1934) in his investigations of the coregonids of Bodensee and other north alpine lakes mentioned repeatedly the distorting effect of the selective action of the gill nets used in taking his samples for the study of age and growth. The effects of the selection were noticeable particularly in the high average lengths determined for the younger, smaller age groups and in the great variation in the relative abundance of the different year classes as determined from the various gill nets used. Wagler held that a close relationship exists between net selection and maximum girth of the individual fish (cf. Lechler, 1929). Elster (1934) in his study of the Blaufelchen (*Coregonus wartmanni*) expressed opinions similar to those of Wagler.

Van Oosten (1929b) in his discussion of the problems of the commercial fisheries of the Great Lakes pointed out the complex nature of the question of selectivity in the gill nets of the commercial fishery and included a small amount of data on the number and size of small trout (*Cristovomer namaycush*) and several species of chubs (*Leucichthys* spp.) taken in $2\frac{1}{2}$ - and $2\frac{3}{4}$ -inch mesh nets.

In a later paper Van Oosten (1933) published a preliminary report of experimental chub net investigations conducted by the United States Bureau of Fisheries in Lake Michigan waters, 1930-32. The data presented included average catch per net, expressed in pounds and number of fish, for the lake trout and the chub in five different sizes of mesh. The meshes used were all of commercial fishery size, and varied from $2\frac{3}{8}$ to 3 inches, stretched measure. The variation in the catch of chubs in nets of different size mesh was striking. In lower Lake Michigan nets of $2\frac{3}{8}$ -inch mesh caught more than twice as many chubs as did nets of $2\frac{1}{2}$ -inch mesh, and eight times as many as nets of 3-inch mesh.

In view of the marked disagreement that the preceding review shows to exist among some authors as to the nature and scope of the selective action of gill nets, it appears probable that each species and each locality offers its own special problem of gear selection.

The selective action of gear as size of mesh affects the amount of total catch (with respect both to numbers and weight) is particularly noteworthy. The existence of an intensive commercial fishery employing a more or less standard size mesh can, however, exaggerate the differences of catch between two different sizes of mesh. Ordinarily all the commercial gear of the same type used in a region for the capture of a species or group of species of similar size will meet approximately the same specifications particularly with reference to the size of mesh. Consequently there tends to be a great reduction in numbers in that portion of the population most liable to capture by the standard commercial gear. The withdrawal of large quantities of commercial size fish produces an abnormal condition in size distribution of the population as a whole. The introduction of nets of other, noncommercial sizes of mesh may then lead to comparisons that do not describe accurately the fishing action of the nets in question. Data based on catches from a population unaffected by commercial fishing might be expected to show somewhat less sharp selectivity than those from a population subjected to heavy fishing. It will be seen that the data of the present investigation tend to support this view.

SELECTIVE ACTION OF GILL NETS USED IN COLLECTING SAMPLES OF CISCOES FROM
TROUT, MUSKELLUNGE, SILVER, AND CLEAR LAKES

In this investigation, although other phases of selectivity will be considered briefly, the study of the selective action of gill nets will be concerned primarily with the effect of selection upon the determination of growth in the various populations. The analysis will involve particularly the comparison of average lengths as determined for a single age group from samples taken in nets of different sizes of mesh. The analyses will show the basis for the elimination of certain selected groups in the computation of general growth curves (see footnote, p. 226) and will furnish a better idea of the validity of the use of gill-net samples in the study of growth. Such analysis is of especial importance here since different ranges of mesh sizes were employed in taking the different years' collections.

Attention should be called to certain criteria that are of general value in determining the reliability of gill-net samples for growth study. It may be pointed out that in general a sparse representation in a sample of a young age group whose average length is near the lower limit of effectiveness of the nets used, is a source of suspicion as to the reliability of the sample of that particular group. If this same sparsely represented group gives calculated growths that are in serious disagreement with those of the older age groups it should be eliminated from the data used for the study of growth in the population as a whole. A further check on the reliability of the material that represents a particular age group lies in the comparison of the average lengths for the group as determined from samples in different sizes of mesh and as determined from the different combinations of such samples. The examination of the length distributions of the catch of nets of different size mesh may also give an idea as to the adequacy of the sampling with respect to particular age groups.

As was mentioned in the introduction the 1928 data do not include records of gear for individual fish. For this reason the 1928 data cannot be used in the study of gill-net selectivity.

For purposes of convenience the gear used in 1928, 1930, and the early part of the 1931 season will be designated throughout this section as "old",³⁶ and the gear used during the latter part of the 1931 season and through the 1932 season will be known as "new." Descriptions of the two groups of nets were included in the section on methods.

Tables 71, 72, 74, 75, 76, and 77 show the effect of size of mesh on the determination of average size of the different age groups in the populations of Trout, Muskellunge, Silver, and Clear Lakes. Because of the generally small number of specimens upon which the average of lengths of the various age groups depend, attention must be given to the general trend of the differences that result from differences in gear rather than to the actual amount of the difference in any specific case. Since each population represents a distinct and separate problem in the study of selectivity, the data for each lake will be discussed separately.

TROUT LAKE

With the exception of a single specimen all the ciscoes collected in Trout Lake in 1930 were obtained from 1½-inch mesh nets, while the 1928 samples were probably taken in nets of 1¼-inch (trammel), 1¾-inch, 1½-inch, and perhaps a few in 1¾- and

³⁶ Although the "old" gear as fished in 1930 and in the early part of 1931 included 5 different sizes of mesh, only the 1½-inch and 2-inch nets caught ciscoes. All collections from Clear Lake were made with the new gear. The date of change in gear was July 22, 1931.

2-inch mesh nets. In 1928 the average length of 182 ciscoes was 138 millimeters, and in 1930 the average length of 490 individuals was 150 millimeters. The smaller average size of the fish of the 1928 collection may be accounted for by the use of mesh sizes smaller than $1\frac{1}{2}$ inches and by the relatively greater abundance of young fish in that year's samples. The relative abundance of the different age groups as well as the average lengths of these age groups in the samples of the 2 years may be found in table 3.

TABLE 71.—*Effect of size of mesh of gill nets on the determination of the average lengths of the age groups of the Trout Lake cisco, 1931 collection*

[The first 2 rows show the average lengths of 5 age groups as based on samples taken July 22 in $1\frac{1}{4}$ - and $1\frac{1}{2}$ -inch mesh gill nets. The third row shows the average of the 2. The fourth row shows the average lengths of the various age groups based on all fish taken in $1\frac{1}{2}$ -inch mesh gill nets in 1931. Sexes combined. Number of specimens in parentheses]

Size of mesh	Age group					Average length
	I	II	III	IV	V	
$1\frac{1}{4}$ inches.....	124 (1)	134 (22)	139 (14)	147 (18)	155 (2)	140 (61)
$1\frac{1}{2}$ inches.....		137 (16)	143 (20)	149 (15)	158 (4)	145 (58)
Averages combined.....	124 (1)	135 (38)	141 (34)	148 (33)	157 (6)	-----
Average of all 1931 $1\frac{1}{2}$ -inch samples.....	132 (1)	137 (39)	142 (159)	148 (246)	156 (77)	147 (522)

A single set of the "new" gear lifted July 22, 1931, provides the only data for Trout Lake for the comparison of growth as based on samples taken in nets with different size mesh. These data appear in table 71. In the first row appear the average lengths for the various age groups as based on fish taken in the $1\frac{1}{4}$ -inch mesh net. The second row gives the same information for the sample from the $1\frac{1}{2}$ -inch mesh net. It will be seen that while the average length of all ciscoes taken in the $1\frac{1}{2}$ -inch mesh net was 5 millimeters greater than that of the ciscoes from the $1\frac{1}{4}$ -inch mesh net, the differences between samples of the same age group varied from 2 to 4 millimeters and averaged only about 3 millimeters. The third row shows the average lengths of the different age groups as based on the combination of the July 22 samples taken in the $1\frac{1}{4}$ - and $1\frac{1}{2}$ -inch mesh nets while the bottom row shows for comparison the average lengths of the various age groups as based on all the ciscoes taken in Trout Lake in the 1931 season in $1\frac{1}{2}$ -inch mesh nets. It may be seen that with the exception of the I group the averages based on the $1\frac{1}{2}$ -inch mesh net samples for the entire season differ but little from those based on the combined catches from $1\frac{1}{4}$ - and $1\frac{1}{2}$ -inch mesh nets. While the necessity for the elimination of the I group from the Trout Lake growth data is at once apparent, the problem presented by the II group requires further consideration. In spite of the rather close agreement between the average length of the II-group fish as determined from samples from nets of $1\frac{1}{4}$ - and $1\frac{1}{2}$ -inch mesh, the sparse representation of this age group in both the 1930 and 1931 collections (table 3) throws suspicion on the reliability of the samples. This suspicion is supported by the high calculated lengths at the end of the first and second years of life as based on both the 1930 and 1931 II groups. Consequently both of the groups were eliminated from the Trout Lake growth data. The II group of 1928, for which year no individual net records are available, was, however, retained, first because of its abundant representation in that year's collection, second because of the good agreement between its calculated growth and the corresponding calculated growth both of older age groups of the same year's collection and of samples of the same (1926) year class taken in the later years, 1930 and 1931, and finally because of the

knowledge that smaller mesh sizes were used in 1928 than in 1930 and the early part of 1931.

The relationship of net size to fish size (new nets, 1931) in the Trout Lake cisco is shown in figure 11.

MUSKELLUNGE LAKE

The old gear was used in the collection of ciscoes from Muskellunge Lake in 1928, 1930, and 1931. In the last 2 years all the fish were taken in the $1\frac{1}{2}$ -inch mesh net. In 1928 the gear used included the following sizes of mesh: $1\frac{3}{8}$ -, $1\frac{1}{2}$ -, $1\frac{3}{4}$ -, and 2-inch. The 2-inch mesh was probably not effective. Data on the average lengths of the various age groups in these years' collections will be found in table 4. In 1932

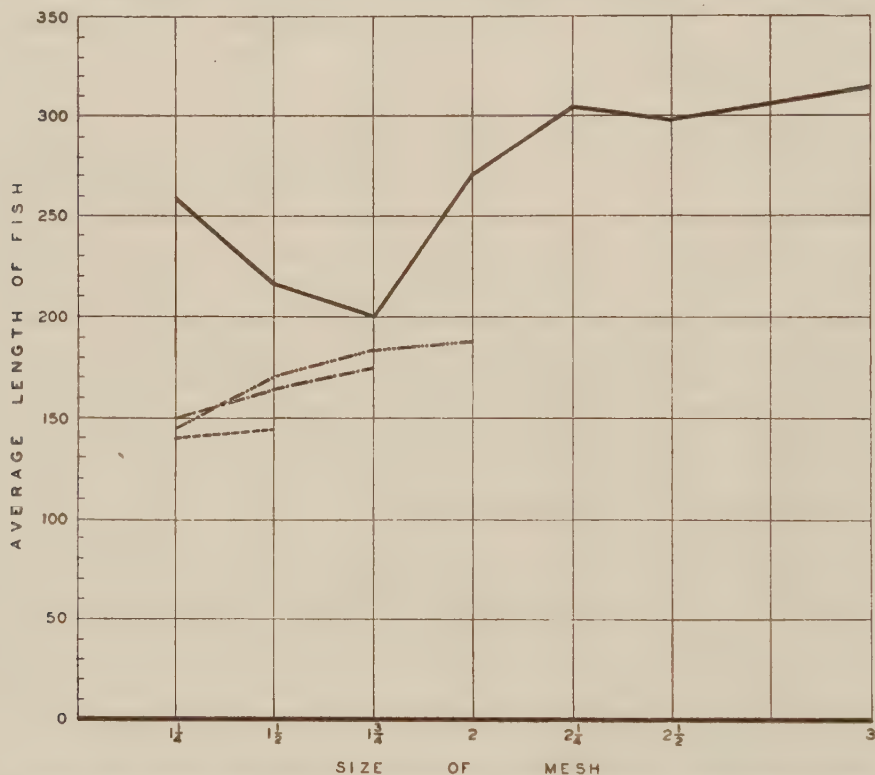


FIGURE 11.—Relationship between size of mesh of gill nets (stretched measure, in inches) and the average standard length in millimeters of the ciscoes taken. $\frac{1}{4}$ Trout Lake, ---; Muskellunge Lake, —; Silver Lake, -.-; Clear Lake, —.

all the specimens were taken in three ($1\frac{1}{4}$ -, $1\frac{1}{2}$ -, and $1\frac{3}{4}$ -inch) of the seven sizes of mesh used in the new gear.

The 1932 material provides the only data for the study of the effect of mesh size on the average size of fish taken and for the comparison of the average lengths of the various age groups as based on samples from nets of different sizes of mesh. Scale examinations were made for 201 specimens of the 1932 collection, but ages could be estimated for only 189 of this number. The results of these determinations appear in table 72.³⁷ The table shows considerable differences between the nets of

³⁷ These data represent all the fish taken in the $1\frac{3}{4}$ -inch mesh net in 1932 and lifts of the $1\frac{1}{4}$ - and $1\frac{1}{2}$ -inch mesh nets on July 28, 29, and 30, and Aug. 3, 1932. The numerical representations of the $1\frac{1}{4}$ - and $1\frac{1}{2}$ -inch mesh nets are comparable, while that for the $1\frac{3}{4}$ -inch net is by comparison too high. This high representation of the $1\frac{3}{4}$ -inch net samples has probably caused the grand average length for the IV group to be too high, but it had little effect on the grand average length for the III group.

different mesh size both in the average size of the fish and in the relative abundance of the different age groups.³³ Selectivity according to length appears to be greater in the Muskellunge Lake cisco, where the 1½-inch mesh net caught fish 14 millimeters longer than the 1¼-inch mesh sample, than in the Trout Lake cisco (table 71) where the fish from the 1½-inch mesh net were only 5 millimeters longer than those from the 1¼-inch mesh net. It will be noticed further that nets of the same size mesh caught larger fish in Muskellunge Lake than in Trout Lake (fig. 11).

TABLE 72.—*Effect of size of mesh of gill nets on the determination of the average lengths of the age groups of the Muskellunge Lake cisco, 1932 collection*

[Sexes combined. Number of specimens in parentheses]

Size of mesh	Age group					Average length
	I	II	III	IV	V	
1¼ inches.....	137 (12)	152 (7)	159 (11)	168 (3)	-----	150 (33)
1½ inches.....	150 (3)	158 (12)	162 (59)	168 (59)	172 (1)	164 (150)
1¾ inches.....	-----	-----	166 (5)	177 (12)	-----	174 (18)
Average.....	139 (15)	156 (24)	162 (75)	170 (74)	172 (1)	-----

The question of the reliability of the 1930 and 1931 collections is largely a question of the reliability of samples from 1½-inch mesh nets, for the collections of these 2 years were taken in nets of this size mesh. The 1928 samples may be considered as reliable as the 1932 samples. The data of table 72 show that in spite of the selection that does occur the 1½-inch mesh net samples, with the exception of the I group, give averages for the lengths of the different age groups that differ insignificantly from the corresponding averages based on the catch of nets of three different sizes of mesh. It is, therefore, a safe conclusion that with the elimination of the I groups the length data obtained from 1½-inch nets in the preceding seasons are accurate within the range of a very few millimeters.

TABLE 73.—*Length frequencies of Muskellunge Lake ciscoes taken in 1932 in nets of different mesh size*

[Sexes combined. The frequencies represent 18 lifts for the 1¼-inch mesh net, 38 for the 1½-inch mesh net, and 37 for the 1¾-inch mesh net]

Length	1¼-inch net	1½-inch net	1¾-inch net	Total	Length	1¼-inch net	1½-inch net	1¾-inch net	Total
185 to 189.....	-----	2	1	3	145 to 149.....	18	48	-----	66
180 to 184.....	-----	6	3	9	140 to 144.....	24	20	-----	44
175 to 179.....	-----	27	4	31	135 to 139.....	40	4	-----	44
170 to 174.....	2	102	6	110	130 to 134.....	7	-----	-----	7
165 to 169.....	5	157	2	164	Total.....	154	813	18	985
160 to 164.....	13	186	1	200	Average length..	146	160	174	-----
155 to 159.....	24	170	1	195					
150 to 154.....	21	91	-----	112					

The above conclusion is supported by the examination of the length frequencies of the total catch of Muskellunge Lake ciscoes in each mesh size in the entire 1932 season (table 73). In the length frequencies of the 1¼-inch net samples there occurs at the 145 to 149 millimeter interval a depression that marks the separation of the I

³³ It was pointed out previously (p. 219), that because of slow growth in the later years and the common occurrence of accessory annuli the separation of the later age groups above the II group in the 1932 Muskellunge Lake samples was difficult. As a consequence, the average lengths listed for the III-group and the IV-group samples may be slightly in error. Any error that exists should not, however, impair greatly the general usefulness of the data for the purpose of studying the effect of net selection on the determination of the average lengths of age groups.

group from fish of greater age. Since the bulk of the II-group fish must lie above this depression it can be seen that their length distribution lies well within the range of efficiency of the 1½-inch mesh net. The fish taken in the 1¾-inch net are so few in number that they would have little effect in the determination of growth.

SILVER LAKE

The "old" gear was used in the collection of all the 1928 and 1930 samples of ciscoes from Silver Lake and for the first sample taken in 1931 (July 17). A gang of the "new" nets was used in taking the only other sample of this year in this lake (Aug. 22, 1931). In the sets of the old gear in 1930 and 1931 ciscoes were taken in 1½- and 2-inch mesh nets only; in 1928 they were probably taken in the 1½- and 1¾-inch meshes also. In the new gear they occurred in the 1¼-, 1½-, 1¾-, and 2-inch mesh nets.

Table 74 shows the average length of fish taken in different mesh sizes and the effect of net selectivity on the determination of the average length of the various age groups of the 1930 collection (5 lifts of 1½-inch nets, 3 of 2-inch nets) while table 75 gives similar information for the 2 lifts made in 1931.

TABLE 74.—*Effect of size of mesh of gill nets on the determination of the average lengths of the age groups of the Silver Lake cisco, 1930 collection*

[Sexes combined. Number of specimens in parentheses]

Size of mesh	Age group					Average length
	II	III	IV	V	VI	
1½.....	173 (7)	178 (16)	182 (34)	190 (4)	198 (1)	186 (66)
2 inches.....		186 (9)	188 (24)	193 (20)	196 (2)	190 (64)
Average.....	173 (7)	181 (25)	183 (58)	193 (25)	197 (3)	

TABLE 75.—*Effect of size of mesh of gill nets on the determination of the average lengths of the age groups of the Silver Lake cisco, 1931 collection*

[The data in the upper part of the table are based on a lift of the "old" nets, July 17. The data in the lower part are based on a lift of the "new" gear, Aug. 22. The grand average for the year includes a number of preserved fish for which no net records were available. Sexes combined. Number of specimens in parentheses]

Size of mesh	Age group							Average length
	I	II	III	IV	V	VI	VII	
1½ inches.....	143 (6)	168 (5)	174 (3)	173 (3)				163 (18)
2 inches.....			189 (3)	187 (5)	192 (14)	198 (5)		191 (29)
Average.....	143 (6)	168 (5)	182 (6)	182 (8)	192 (14)	198 (5)		
1¾ inches.....	141 (51)	172 (3)	175 (3)	172 (1)	185 (2)			146 (60)
1½ inches.....	146 (6)	170 (6)	176 (4)	173 (6)	187 (7)			171 (30)
1¾ inches.....		174 (2)	178 (22)	182 (25)	186 (23)	193 (4)		183 (83)
2 inches.....			174 (1)	184 (12)	190 (18)	192 (2)	201 (1)	188 (37)
Average.....	142 (57)	171 (11)	177 (30)	181 (44)	188 (50)	193 (6)	201 (1)	
Grand average for 1931.....	142 (66)	171 (19)	177 (61)	183 (102)	188 (108)	194 (21)	201 (1)	

The data in tables 74 and 75 show rather large differences in the average size of fish taken in nets of different sizes of mesh. Although the fish taken in the 2-inch-mesh net of the old gear in 1930 were only 4 millimeters longer than those taken in the 1½-inch net, the 1931 samples taken in the same gear showed a difference of 28 millimeters, while the 2-inch-mesh net fish of the 1931 collection in the new gear had an average length 17 millimeters above the average for those from the 1½-inch net. A comparison with the Trout Lake and Muskellunge Lake data (tables 71 and 72, fig. 11) shows that the selection of the nets is sharper in the Silver Lake cisco than

in either of the former populations. The difference in average length between fish taken in $1\frac{1}{2}$ - and $1\frac{3}{4}$ -inch-mesh nets was for example 5 millimeters in Trout Lake, 14 millimeters in Muskellunge Lake, and 25 millimeters in Silver Lake. Further, the difference in average length between fish taken in $1\frac{1}{2}$ - and $1\frac{3}{4}$ -inch-mesh nets in Muskellunge Lake was 10 millimeters while in the Silver Lake cisco this difference was 12 millimeters.

Tables 74 and 75 show also that the average length for a particular age group varies considerably in samples taken by nets of different size mesh. Although certain irregularities occur (as might be expected from the small size of the samples) there is a general tendency for the samples from larger mesh nets to show distinctly higher average lengths for a given age group than do the samples from nets of smaller mesh. Further examination shows, however, that this tendency does not in general affect the validity of the averages of age groups based on the combination of the samples of several nets.

In the analysis of the data of tables 74 and 75 to establish the validity of the growth data for the Silver Lake cisco, it should be pointed out first that all ages above the II group in the 1931 sample taken in the new nets must be considered to have adequate representation throughout their entire length range. This is apparent from the fact that these older age groups are relatively scarce in the $1\frac{1}{4}$ -inch-net catch, while at the other extreme a $2\frac{1}{4}$ -inch-mesh net that was fished in the string failed to take any ciscoes at all. Since these average lengths of the older age groups from the new net sample can be considered reliable they can be used as a basis for the estimation of the reliability of the corresponding average lengths as determined from the old net samples. The fact that the average lengths for corresponding age groups of the 1930 and 1931 old net collections resemble each other on the whole more than either of them resembles the average lengths based on the 1931 new net collection suggests that the addition of the $1\frac{1}{2}$ - and $1\frac{3}{4}$ -inch nets may have increased the reliability of the Silver Lake samples. The differences between the corresponding average lengths of the older age groups of the old and new net samples are not, however, of sufficient magnitude to invalidate the use of the earlier materials collected by the old gear.

The II-group samples present a more difficult problem. The general scarcity of II-group individuals in the collections of the old gear would indicate that its length range may lie just below the range of efficiency of the $1\frac{1}{2}$ -inch net, even though this size mesh was very efficient in Trout and Muskellunge Lakes in the taking of fish whose lengths were well below the observed average length (about 170 millimeters) for the Silver Lake II group. The 1931 sample with the new gear shows, however, that it is very unlikely that the Silver Lake II group has suffered serious selection by gear, as that selection affects average length, in any of the samples. The scarcity of the II-group fish in this sample taken in the new gear must be considered to show that this group in 1931 actually was less abundant than the neighboring age groups, for there is no reason to hold that the same nets that took 57 I-group and 30 III-group fish should fail to take II-group individuals in equal numbers provided they were equally abundant in the population. These facts together with the good agreement between the average lengths of the II-group samples as based on old and new gear samples make the retention of the II-group fish in the growth data advisable.

Since there is no means of demonstrating the reliability of any of the I-group samples they must be considered, at the best, questionable. They were accordingly eliminated from the growth data.

CLEAR LAKE

All Clear Lake specimens were collected with the "new" nets. Tables 76 and 77 show the average lengths of the different age groups according to the gear by which they were captured. Because of differences in growth rate the sexes are treated separately. Table 78 and figure 11 present the length frequencies and the average length of the catch according to mesh size for the total 1931 and 1932 catch of ciscoes from Clear Lake. The Clear Lake data differ from those of the three populations just considered in two important respects. First, the relationship that increase in size of mesh is correlated with an increase in the average size of the fish taken does not hold for Clear Lake as it did in the other three lakes; while the differences in the average size of the fish taken in different meshes are great, the larger mesh does not always take the larger fish (table 78, fig. 11). Second, in Clear Lake, fish were taken in all seven of the sizes of mesh used, and were most abundant in nets that were totally ineffective in all the other three populations, that is, nets whose mesh size was greater than 2 inches. The circumstance that the largest mesh (3 inches) took the greatest number of fish indicates that in making these collections it would have been desirable to use additional nets of mesh size greater than 3 inches. There is, however, reason to believe that the selection resulting from failure to fish with larger mesh nets affects chiefly the relative abundance of the larger fish in the sample. The increase in size of mesh from 2¼ to 3 inches had little effect on the average length of the individuals captured. If this trend were to continue, nets of a mesh size greater than 3 inches would be expected to add to the number of large fish without producing any important upward extension of the size range of the sample.

TABLE 76.—*Effect of size of mesh of gill nets on the determination of the average lengths of the age groups of the Clear Lake cisco, 1931-32 collections*

[(Males) Number of specimens in parentheses]

Size of mesh	Age group									Average length
	I	II	III	IV	V	VI	VII	VIII	IX	
1½ inches.....	173 (12)			311 (1)			336 (3)			212 (16)
1¾ inches.....	176 (24)	236 (3)	254 (1)							185 (28)
2 inches.....	190 (2)	245 (3)	291 (4)		307 (3)	310 (1)		341 (1)		275 (14)
2¼ inches.....		260 (12)	286 (5)	314 (4)	328 (4)	326 (2)	333 (5)	347 (3)		296 (35)
2½ inches.....		266 (25)	289 (12)	319 (6)		328 (2)	329 (1)	334 (2)	355 (1)	281 (49)
3 inches.....		267 (5)	291 (18)	324 (4)	338 (2)	324 (3)	334 (6)	344 (4)		307 (42)
Average.....	176 (38)	264 (48)	289 (40)	318 (15)	323 (9)	324 (8)	334 (15)	343 (10)	355 (1)	

TABLE 77.—*Effect of size of mesh of gill nets on the determination of the average lengths of the age groups of the Clear Lake cisco, 1931-32 collections*

[(Females) Number of specimens in parentheses]

Size of mesh	Age group											Average length
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	
1½ inches.....	155 (1)							336 (1)				246 (2)
1¾ inches.....	179 (5)							350 (1)				245 (8)
1¾ inches.....	180 (12)	279 (1)					356 (3)	357 (1)	351 (1)	364 (1)		227 (17)
2 inches.....	186 (7)	293 (7)	301 (1)	325 (1)	338 (1)		336 (1)	360 (3)	376 (1)			268 (22)
2¼ inches.....	201 (1)	259 (4)	300 (9)	323 (3)		371 (1)	351 (9)	360 (2)				316 (29)
2½ inches.....		265 (14)	308 (14)	332 (5)	335 (3)	342 (4)	357 (6)	351 (7)			378 (1)	315 (54)
3 inches.....		260 (14)	310 (15)	332 (8)	347 (4)	334 (4)	350 (11)	358 (7)	352 (1)	379 (1)		319 (65)
Average.....	181 (26)	263 (40)	307 (39)	330 (17)	341 (8)	342 (9)	352 (30)	355 (22)	360 (3)	372 (2)	378 (1)	

TABLE 78.—*Length frequencies of Clear Lake ciscoes taken in nets of different mesh size*

[The 1931 and 1932 collections and the sexes are combined]

Length	1¼ inches	1½ inches	1¾ inches	2 inches	2¼ inches	2½ inches	3 inches	Total
150 to 159	1							1
160 to 169		4	6					10
170 to 179		10	17	3				30
180 to 189		3	12	3				18
190 to 199			1	2				2
200 to 209			1	1	1			3
210 to 219			1					1
220 to 229								1
230 to 239				2	1			5
240 to 249			2		1	8		11
250 to 259			1	4	7	12	8	32
260 to 269				2	5	11	8	26
270 to 279				3	1	9	4	17
280 to 289	1			2	2	4	7	16
290 to 299					4	8	10	22
300 to 309				2	8	6	6	22
310 to 319		1		3	4	12	13	33
320 to 329				2	7	6	11	26
330 to 339	1	2		2	6	7	12	30
340 to 349		1	1	1	4	10	12	29
350 to 359		2	2	2	3	6	10	25
360 to 369		1	1		5	1	5	13
370 to 379				1	2	2	1	6
380 to 389						1	1	2
Total	3	24	44	35	64	103	108	382
Average length	259	217	201	271	306	299	315	

The Clear Lake samples with the exception of the I groups do not show as close dependence between the determination of the average length of individual age groups and the size of mesh by which the sample was taken (tables 76 and 77) as was observed in the other three populations. The proof of the reliability of the Clear Lake growth data must be based, therefore, on a demonstration that the population was adequately sampled throughout its length range rather than on a comparison of the average lengths of age groups as determined from samples from nets of different mesh size. It was pointed out in the preceding paragraph that the sampling of the larger fish was probably adequate. The scarcity of fish in the 1¼-inch net can be taken to show that the younger age groups were also adequately sampled. Accordingly, no age groups were eliminated from the Clear Lake samples.

RELATIVE ABUNDANCE OF AGE GROUPS IN GILL NET SAMPLES

The examination of tables 71, 72, 74, 75, 76, and 77 shows that on the whole the selectivity of nets is much more sharp in its effect on the number of fish in a given age group than in its effect on the determination of the average length of that age group. The following examples will illustrate this point. In Muskellunge Lake (table 72) the average lengths of the III-group fish in the 1¼- and 1½-inch-mesh nets were 159 millimeters and 162 millimeters, respectively; however, the 1¼-inch net took only 11 fish of this age group while the 1½-inch net took 59. In Silver Lake (table 75, data on lift of new nets) the III-group sample of the 1½-inch mesh had an average length only 2 millimeters less than the III-group sample from the 1¼-inch net, but was nevertheless represented by only 4 fish as compared with the 22 fish from the 1¼-inch-mesh net. In the same day's collection the V-group samples from the same two sizes of mesh had practically identical average lengths, but were more than three times as numerous in the 1¼-inch-mesh net as in the 1½-inch net. In Clear Lake (tables 76 and 77) the fish of the older age groups were more abundant in the samples of the 2½- and 3-inch-mesh nets, but the average lengths of these older age groups as determined from 2½- and

3-inch-net samples failed to be consistently higher than the average lengths determined for the same age groups from samples that were taken in smaller meshes.

From the above examples it may be concluded that selection by numbers is much sharper than selection by length. Apparently nets of different mesh size, which in their operation upon a population take samples that disagree only slightly as to average length, may take their samples with unequal degrees of facility, with the result that while their catches agree closely in average length they may differ markedly as to the actual number of fish taken. Table 78 (catch of 2¼-, 2½-, and 3-inch nets) shows such a situation. If small differences in the sizes of mesh are accompanied by large differences in the number of fish captured from a certain size range, then small differences in the average sizes of different groups of fish may be expected to produce large differences in their numerical abundance in the catch of a particular size mesh.

From the above conclusions it can be seen that a series of nets that may take quite reliable samples of particular age groups, as average length is concerned, may at the same time fail to capture the members of these age groups in numbers corresponding to their actual relative abundance in the population of which they are part. Consequently gill-net samples must be employed with extreme caution in the study of the relative abundance of age groups and year classes.

GENERAL CONCLUSIONS

If the collections from the four lakes are considered as a whole it may be stated that the action of a gill net of specified mesh is predictable only with reference to the specific nature of the population to be sampled. The action of a net of specified mesh depends first upon the range of length and abundance of the fish within the population and second upon those morphological characteristics that determine in what manner the fish is held captive. A demonstration of the reliability of a sample obtained by use of gill nets from one population does not indicate that the same gear will obtain an equally reliable sample from a second, different population.

On the question of the use of gill-net samples for growth studies it was demonstrated that the analysis of growth data with respect to size of mesh of the gear in which samples are taken aids in the detection of age groups whose appearance in the sample is by reason of selection not representative. These age groups should be eliminated completely from the data. Such selected age groups were detected in three of the four populations considered here. It was demonstrated further that if these selected groups are eliminated the remaining growth data can be considered accurate and trustworthy within very narrow limits. No such high degree of reliability can be claimed for gill-net samples in the study of the relative abundance of the different age groups.

SUMMARY

1. This study of the growth of the cisco was based on the determination of age of 3,882 specimens and the calculation of growth from scale measurements of 3,694 specimens. The data for Trout, Muskellunge, Silver, and Clear Lakes are presented in the general paper while the smaller samples from Allequash and Tomahawk Lakes are treated separately in an appendix.

2. It was assumed that Van Oosten's (1929) demonstration of the validity of the scale method in *Leucichthys artedi* can be considered to apply to the four cisco popu-

lations of the present investigation. The consistent results obtained appear to justify the assumption.

3. The calculation of growth from scale measurements was based on the assumption that body length and scale diameter show a constant ratio at all lengths beyond that at which the first annulus is laid down. In the Silver Lake cisco alone were there any discrepancies between growth as calculated from fish of different age and as determined empirically that might throw doubt on the validity of the assumption.

4. It was demonstrated that Lee's phenomenon in the Silver Lake cisco does not depend on changing body-scale relationships with increase in length and age, but rather that the growth discrepancies are reflected in the actual scale measurements upon which the calculated growths were based.

5. Among the suggestions for the explanation of Lee's phenomenon in the Silver Lake cisco were: (1) Selection by gear, (2) selection due to dissimilar distribution within the lake of the various elements of the population, and (3) selection due to differential mortality correlated with individual growth rate (greater mortality among individuals with more rapid growth).

6. The four populations (Trout Lake, Muskellunge Lake, Silver Lake, and Clear Lake ciscoes) show wide differences in the amount and rate of growth both in length and weight. Their order with respect to growth rate in length, from minimum to maximum, is: Trout Lake, Silver Lake, Muskellunge Lake, Clear Lake; the order with respect to growth in weight is: Trout Lake, Muskellunge Lake, Silver Lake, Clear Lake.

7. On the basis of data on the growth of the cisco in this and other publications a "cisco-type" of growth was described.

8. On the whole the high degree of overlap of the length distributions of consecutive age groups of the cisco makes length alone a poor index of age.

9. Because of individual variation in growth rate the largest fish within a population is frequently not the oldest.

10. Condition was described in terms of the quantity K in the equation, $W=K \times 10^{-5} L^3$ (W =weight in grams; L =length in millimeters). It was pointed out that coefficients of condition calculated from the cube relationship describe relative heaviness independently of the general length-weight relationship, and are more satisfactory measures of condition than the quantity C in the equation $W=CL^n$ where the value of n is determined empirically.

11. The four cisco populations show wide differences with respect both to average condition and the manner of change of condition with change in length. The Muskellunge Lake cisco and the Trout Lake cisco show a loss of condition with increase in length (the rate of loss of condition is the more rapid in the former population). The Silver Lake cisco and the Clear Lake cisco, on the other hand, show improvement of condition with increase in length (the rate of improvement in condition is the greater in the Clear Lake cisco). The order of the four lakes with respect to the average condition of the fish in the samples, from minimum to maximum, is: Muskellunge Lake, Trout Lake, Silver Lake, Clear Lake.

12. In all four populations the relationship between length and weight may be described over certain length intervals by equations of the type, $W=CL^n$, where W =weight, L =length, and C =a constant. In some of the populations, at least, these equations cannot be extended to lengths outside the range of the empirical data.

13. The approximate date at which the season's growth of the cisco is completed in each of the lakes is: Trout Lake, end of July; Muskellunge Lake, late August; Silver Lake, early September; Clear Lake, late September or early October. Growth probably begins in all four populations shortly after the disappearance of the ice at about the 1st of May. The data show that the length of the cisco's growing season depends on the local conditions within each lake and not on the climatic conditions that are approximately the same for all four lakes.

14. The bathymetric distribution of the cisco in middle and late summer is highly sensitive to conditions of temperature and dissolved oxygen concentration. A knowledge of the vertical distribution of the cisco is important in the comparison of the densities of the populations of different lakes.

15. The order of the four lakes with respect to the density of their cisco populations, from the minimum to the maximum, is: Clear Lake, Silver Lake, Muskellunge Lake, Trout Lake.

16. The large differences observed in the relative abundance of the various year classes show that the degree of success of the hatch of the cisco in different calendar years is subject to a wide range of variation. Since the years that saw relatively successful or unsuccessful hatches of the cisco are not the same in different lakes, it must be concluded that the relative abundance of a particular year class depends (as does the length of the growing season) on the local conditions within each individual lake, and not on general climatic conditions that would affect all lakes in the same manner.

17. In the Clear Lake cisco sexual maturity appears to be general at the end of the second year of life. In the other populations the cisco is known to be mature at the end of the third year of life, while some, at least, mature in the second year.

18. The order of the four lakes with respect to the sex ratio of the cisco populations (expressed as the number of females per 100 males), from minimum to maximum, is: Clear Lake, Silver Lake, Muskellunge Lake, Trout Lake. The differences among the populations with respect to the sex ratio depend on differences in the differential rates of mortality of the two sexes.

19. The available data indicate a close connection between certain phases of the life history of the cisco and the nature of its animate and inanimate environment.

20. The order of the four lakes with respect to the rate of growth of their cisco populations (in weight) is the same as their order with respect to the length of the cisco's growing season, and the reverse of their order with respect to the density of their cisco populations.

21. The observed differences in the length of the cisco's growing season in different lakes cannot account entirely for the observed differences in growth rate, but probably serve only to accentuate differences that already exist.

22. Suggested explanations of differences in the length of the cisco's growing season in different lakes were: (1) That they may depend on differences from lake to lake in the nature of the plankton cycle, and (2) that the smaller spawners of slow-growing populations may begin the development of the gonads, preliminary to autumn spawning, earlier in the season than do the larger spawners of the rapidly growing populations. (The four lakes follow the same order with respect to growth rate, length of the growing season, and the average size of mature fish.)

23. The correlation between density of population and growth rate may depend on differences in the severity of the competition for food, or upon the operation of a

"space-factor", whereby crowding alone impedes growth independently of the abundance of food.

24. Since, with the exception of a reversal of the positions of the closely similar Muskellunge Lake and Silver Lake populations, the four lakes arrange themselves in the same order with respect to the density of their cisco populations and with respect to the concentration of bound CO_2 in their waters, it was suggested that differences (traceable to the concentration of bound CO_2) in the kind and abundance of plankton available to newly hatched ciscoes may account for the observed differences in the densities of the four cisco populations.

25. Although the relationship between parasite infestation and growth rate has not been thoroughly investigated in the cisco it is known that the Clear Lake cisco, which has by far the best growth of any of the four populations, is practically free of parasites (96 percent negative), while the slower-growing populations from Silver, Muskellunge, and Trout Lakes have a heavy infestation of intestinal parasites (80 percent, or more, positive).

26. The best growth of the cisco occurs in Clear Lake with the smallest amount of organic matter in the surface plankton, but Muskellunge Lake, with the greatest amount of organic matter in the surface plankton does not have the slowest-growing cisco population.

27. The order of the four lakes with respect to the value of the sex ratio (females per 100 males) is the reverse of their order with respect to the rate of growth (in weight). It was suggested that the same factors that determine the rates of growth may cause the differential mortality rate of the less viable males to be greater in the slower-growing populations.

28. The Clear Lake cisco with the most rapid growth is in the best average condition (highest average value of K) and shows the most rapid improvement of condition with increase in length, but the Muskellunge Lake cisco with the poorest average condition and the most rapid loss of condition with increase in length is not the population with the slowest growth.

29. The at least partial independence of the factors that determine growth rate and the factors that determine condition may be construed as a strong argument for the operation of the "space-factor" in the determination of growth rate.

30. The order of the four lakes with respect to the average condition of their cisco populations and the rate of change of condition with increase in length is the reverse of their order with respect to the abundance of organic matter in the surface plankton. Thus it appears that the poorest condition is found in the most eutrophic environment and the best condition in the most oligotrophic environment.

31. Longevity and condition appear to be correlated. The average life span of the cisco is shortest in Muskellunge Lake where the average condition (K) is poorest and increase in length is accompanied by a rapid loss of condition, and the longest in Clear Lake where the average condition is best and condition improves as length increases.

32. In a general review and summary of the growth relationships of the cisco, it was brought out that some of these relationships fail to conform to generally accepted theories. The need was mentioned for a broader knowledge of the biology of the cisco based on observations in a great diversity of habitats. Attention was called to the danger of premature generalizations concerning the growth relationships and the biology of this very plastic species.

33. In each cisco population the amount of growth made by fish in the same year of life but in different calendar years was found to vary considerably. There is no apparent correlation between these variations in the amount of growth in different calendar years and annual variations in the average air temperature during the growing season. There is some indication that annual fluctuations in the density of each individual population may affect the amount of growth made in different calendar years, but with the possible exception of Clear Lake the data in support of such a relationship are not convincing.

34. The 1928 year class of Trout Lake and the 1926 and 1928 year classes of Muskellunge Lake show a bimodal distribution of the calculated lengths at the end of the first year of life. It was suggested that the reason for these bimodal distributions lies in exceptional weather conditions that bring about two hatchings in the spring. However, the effectiveness of weather conditions in bringing about two hatchings appears to depend on local conditions within each lake.

35. The 1928 year class in Muskellunge Lake which has a bimodal distribution of the calculated lengths at the end of the first year of life, and the 1929 Muskellunge Lake year class, which has an unimodal distribution of the calculated lengths at the end of the first year of life, were used as the basis of a study of the effect of the distribution of lengths at an early stage in the life history on the phenomenon of growth compensation in later years. It was found that growth compensation is much more intense in the group with the greater dispersion of the length distribution at the end of the first growing season. In both groups the larger fish at the end of the first year of life tend to be the larger fish at the end of the second year of life and at the time of capture in the third or fourth summer. Growth compensation in later years reduces the advantage of the large first year fish but fails to eliminate it completely.

36. The fish associations of which the ciscoes are part vary from lake to lake. In midsummer the cisco is taken in Trout Lake only with the typical deep water forms, the whitefish, the lake trout, and the burbot; in Muskellunge Lake large numbers of perch and other shallow-water fish are taken with the cisco; in Silver Lake the cisco spends the summer in practical isolation; and in Clear Lake the pike-perch is relatively abundant in the strata inhabited by the cisco.

37. Because of the scattered nature of the available published data, a review was made of earlier investigations concerning the selective action of gill nets.

38. The examination of the size and age composition of the gill-net samples showed that the action of a net or group of nets in taking samples of a cisco population cannot be predicted on the basis of experiences with other populations of the same species, but that each population presents its own problem of gill-net selectivity. Although gill nets are very selective in their operation, the judicious elimination of selected age groups can make gill-net samples highly reliable for the determination of growth curves. Extreme caution must be employed, however, in the use of gill-net samples for the study of age and year class composition.

BIBLIOGRAPHY

- BIRGE, EDWARD A., and CHANCEY JUDAY. 1911. The inland lakes of Wisconsin. The dissolved gases of the water and their biological significance. Wisconsin Geol. and Nat. Hist. Sur., Bull. XXII, Scientific Series No. 7, 1911. xx+259 pp. Madison.
- BJERKAN, P. 1917. Age, maturity, and quality of North Sea herrings during the years 1910-13. Report, Norwegian Fish. and Mar. Inves., vol. III, no. 1, 1917, 119 pp. Bergen.
- BLEGVAD, H. 1933. Plaice transplantation. Jour. du Cons., Cons. Perm. Internat. Explor. Mer, vol. VIII, no. 2, 1933, pp. 161-180. Copenhagen.

- BORLEY, J. O. 1912. Report on the experimental transplantation of plaice to the Dogger Bank carried out by the Marine Biological Association in the years 1904-08. Internat. Fish. Invest., Report IV (Southern Area Cd. 6125), 1912, 79 pp. London.
- BORLEY, J. O., and E. S. RUSSELL. 1922. Report on herring trawling. Min. Agri. and Fish., Fishery Investigations, series II, vol. IV, no. 4, 1922, 57 pp., 12 figs. London.
- BOWMAN, ALEXANDER. 1932. The effect on the stock of the capture of undersized fish. The haddock population of the North Sea plateau. Rapp. et Procès-Verb., Cons. Perm. Internat. Explor. Mer, vol. LXXX, no. III, 1932, 19 pp. Copenhagen.
- BUCHANAN-WOLLASTON, H. J. 1927. On the selective action of a trawl net, with some remarks on the selective action of drift nets. Jour. du Cons., Cons. Perm. Internat. Explor. Mer, vol. II, no. 3, 1927, pp. 343-355. Copenhagen.
- BÜCKMANN, ADOLF. 1932. Die Frage nach der Zweckmässigkeit des Schutzes untermässiger Fische und die Voraussetzungen für ihre Beantwortung. Rapp. et Procès-Verb., Cons. Perm. Internat. Explor. Mer, vol. LXXX, no. VII, 1932, 16 pp. Copenhagen.
- CAHN, ALVIN ROBERT. 1927. An ecological study of southern Wisconsin fishes. The brook silversides (*Labidesthes sicculus*) and the cisco (*Leucichthys artedii*) in their relations to the region. Illinois Biol. Mono., vol. XI, no. 1, 1927, 151 pp., 16 plates. Urbana.
- CLARK, FRANCES N. 1928. The weight-length relationship of the California sardine (*Sardina caerulea*) at San Pedro. Division of Fish and Game of California, Fish Bull. No. 12, 1928, 59 pp., XI figs. Sacramento.
- CLEMENS, WILBERT A. 1922. A study of the ciscoes of Lake Erie. University of Toronto Studies, Publications, Ontario Fish. Res. Lab., No. 2, 1922, pp. 27-37. Toronto.
- CREASER, CHARLES W. 1926. The structure and growth of the scales of fishes in relation to the interpretation of their life history, with special reference to the sunfish *Eupomotis gibbosus*. Museum of Zoology, University of Michigan, Misc. Pub., no. 17, Dec. 15, 1926, pp. 1-82, 12 pl., 12 figs. Ann Arbor.
- CROZIER, WILLIAM J., and SELIG HECHT. 1914. Correlation of weight, length, and other body measurements in the weakfish, *Cynoscion regalis*. Bull., Bur. Fish. vol. XXXIII, 1913 (1915), pp. 139-147, 4 figs. Washington.
- DAWES, BEN. 1930. Growth and maintenance in the plaice (*Pleuronectes platessa* L.). Part I. Jour., Marine Biol. Asso., United Kingdom, N. S., vol. XVII, no. 1, 1930, pp. 103-174, 19 figs. Plymouth.
- DAWES, BEN. 1931a. Growth and maintenance in the plaice (*P. platessa* L.). Part II. Jour., Marine Biol. Asso., United Kingdom, N. S., vol. XVII, no. 3, 1931, pp. 877-947, 11 figs. Plymouth.
- DAWES, BEN. 1931b. A statistical study of growth and maintenance in the plaice (*P. platessa* L.). Jour., Marine Biol. Asso., United Kingdom, N. S., vol. XVII, no. 3, 1931, pp. 949-976, 5 figs. Plymouth.
- DELSMAN, H. C. 1914. Über das Wachstum von Nordseehering und Zuiderseehering nach Untersuchungen an den Schuppen. Rapporten en Verhandelingen. Uitgegeven door het Rijksinstituut voor Visscherijonderzoek, Deel I, aft. 2, 1914, pp. 133-200, 4 figs., II pls. S. Gravenhage.
- DYMOND, J. R. 1933. Biological and oceanographic conditions in Hudson Bay. 8. The coregonine fishes of Hudson and James Bays. Contrib., Canadian Biol. and Fish., N. S., vol. VIII, no. 1 (Series A, General, No. 28), 1933, pp. 1-12. Toronto.
- ELSTER, HANS-JOACHIM. 1934. Beiträge zur Biologie des Blaufelchen (*Coregonus wartmanni* Bloch). Internationale Revue der gesamten Hydrobiologie und Hydrographie, Bd. 30, 1934, S. 181-246, 6 figs. Leipzig.
- FOREL, F. A. 1892. Le Leman. Monographie limnologique, 3 vols., 1892. Lausanne.
- FRASER, J. H. 1931. On the size of *Urosalpinx cinerea* Say with some observations on the weight-length relationship. Proc., Malacological Soc., vol. XIX, part V, 1931, pp. 243-254. London.
- FULTON, T. WEMYSS. 1904. The rate of growth of fishes. Twenty-second Annual Report, Fish. Bd., Scotland, 1903 (1904), part III, pp. 141-241. Edinburgh.
- GARSTANG, WALTER. 1926. Plaice in the North Sea—changes in size of catch. The London Times, 1926, April 21, p. 15; April 26, p. 20. London.
- GEISER, S. W. 1923. Evidences of a differential death rate of the sexes among animals. American Midland Naturalist, vol. VIII, no. 7, 1923, pp. 153-163. St. Louis.
- GEISER, S. W. 1924a. Sex ratios and spermatogenesis in the top-minnow, *Gambusia holbrooki* Grd. Biol. Bull., vol. XLVII, no. 3, 1924, pp. 175-212. Woods Hole.

- GIESER, S. W. 1924b. The differential death rate of the sexes among animals, with a suggested explanation. Washington University Studies, vol. XII, series no. 1, 1924, pp. 73-96. St. Louis.
- HAACKH, THEODOR. 1929. Studien über Alter und Wachstum der Bodenseefische. Archiv für Hydrobiologie, Bd. 20, Heft 2, 1929, S. 214-295. Berlin.
- HART, JOHN L. 1928. Data on the rate of growth of pike perch (*Stizostedion vitreum*) and sauger (*S. canadense*) in Ontario. University of Toronto Studies, Publications, Ontario Fish. Res. Lab., no. 34, 1928, pp. 45-55, 3 figs. Toronto.
- HART, JOHN L. 1931. The growth of the whitefish, *Coregonus clupeaformis* (Mitchill). Contrib., Canadian Biol. and Fish., N. S., vol. VI, no. 20 (series A, general, no. 5), April 8, 1931, pp. 429-444, 11 figs. Toronto.
- HART, JOHN L. 1932. Statistics of the whitefish (*Coregonus clupeaformis*) population of Shesapeake Island Lake, Ontario. University of Toronto Studies, Publications, Ontario Fish. Res. Lab., no. 42, 1932, pp. 1-28. Toronto.
- HECHT, SELIG. 1916. Form and growth in fishes. Contrib., Zoological Laboratory, Museum of Comparative Zoology, Harvard College, Cambridge, no. 275. Jour. Morphology, vol. XXVII, no. 2, 1916, pp. 379-400. Philadelphia.
- HEINCKE, F., and A. BÜCKMANN. 1926. Die Ueberfischung der Nordsee und die Wirkungen der Kriegsschönzeit auf ihren Schollenbestand. Der Fischerbote. Norddeutsche Fischerei-Zeitung, XVIII, Jahrg. 1926, S. 57-101, 13 figs. Hamburg.
- HIGGINS, ELMER. 1928a. Progress in biological inquiries, 1926. Including proceedings of the divisional conference January 4-7, 1927. Appendix VII, Report, U. S. Comm. Fish., 1927 (1928), pp. 517-681. Washington.
- HIGGINS, ELMER. 1928b. Progress in biological inquiries, 1927. Appendix VI, Report, U. S. Comm. Fish. 1928 (1929), pp. 199-247. Washington.
- HIGGINS, ELMER. 1930. Progress in biological inquiries, 1928, including extracts from the proceedings of the divisional conference, January 2 to 5, 1929. Appendix X, Report, U. S. Comm. Fish., 1929 (1930), pp. 627-739. Washington.
- HIGGINS, ELMER. 1931a. Progress in biological inquiries, 1929. Appendix XV, Report, U. S. Comm. Fish., 1930 (1931), pp. 1069-1121, 11 figs. Washington.
- HIGGINS, ELMER. 1931b. Progress in biological inquiries, 1930. Appendix III, Report, U. S. Comm. Fish., 1931 (1932), pp. 553-626, 9 figs. Washington.
- HIGGINS, ELMER. 1932. Progress in biological inquiries, 1931. Appendix III, Report, U. S. Comm. Fish., 1932 (1933), pp. 441-529. Washington.
- HIGGINS, ELMER. 1933. Progress in biological inquiries, 1932. Appendix II, Report, U. S. Comm. Fish., 1933 (1934), pp. 79-147. Washington.
- HILE, RALPH. 1931. The rate of growth of fishes of Indiana. Investigations of Indiana Lakes, No. 2. Depart. Conser., Division of Fish and Game, Indiana, Publication No. 107, 1931, pp. 9-55. Indianapolis.
- HJORT, JOHAN. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. et Procès-Verb., Cons. Perm. Internat. Explor. Mer, vol. XX, 1914, 288 pp., 137 figs. Copenhagen.
- HJORT, JOHAN. 1926. Fluctuations in the year classes of important food fishes. Jour. du Cons., Cons. Perm. Internat. Explor. Mer, vol. 1, no. 1, 1926, pp. 5-38, 18 figs. Copenhagen.
- HJORT, JOHAN. 1932. Remarks on the fluctuations in number and growth in marine populations. Rapp. et Procès-Verb., Cons. Perm. Internat. Explor. Mer, vol. LXXX, no. IX, 1932, pp. 3-8. Copenhagen.
- HODGSON, W. C. 1927. Preliminary note on experiments concerning the selective action of drift nets. Jour. du Cons., Cons. Perm. Internat. Explor. Mer, vol. II, no. 3, 1927, pp. 356-360, 3 figs. Copenhagen.
- HODGSON, W. C. 1933. Further experiments on the selective action of commercial drift nets. Jour. du Cons., Cons. Perm. Internat. Explor. Mer, vol. VIII, no. 3, 1933, pp. 344-354. Copenhagen.
- HUITFELDT-KAAS, HARTWIG. 1917. Mjøsens fisker og fiskerier. Det Kgl. Norske Videnskabers Selskabs Skrifter, Nr. 2, Heft 1, 1916 (1917), iv+257 S. Trondhjem.
- HUITFELDT-KAAS, HARTWIG. 1927. Studier over aldersforholde og veksttyper hos norske ferskvannsfisker. Nationaltrykkeriet, 1927, S. 5-358. Oslo.

- IRELAND FISHERIES. 1905. Report on the sea and inland fisheries of Ireland for 1902 and 1903. Part II. Scientific Investigations. Depart. of Agric. and Tech. Instruct., Ireland, 1905, 385 pp., XXXV pls. Dublin.
- JÄRNEFELT, H. 1921. Untersuchungen über die Fische und ihre Nahrung im Tuusulasee. Acta Societatis Pro Fauna et Flora Fennica, vol. 52, no. 1, 1921, 160 pp. Helsinki.
- JÄRVI, T. H. 1920. Die kleine Maräne (*Coregonus albula* L.) im Keitelesee, eine ökologische und ökonomische Studie. Annales Academiae Scientiarum Fennicae, Serie A, vol. XIV, No. 1, 1920, 302 pp. Helsinki.
- JÄRVI, T. H. 1924. Die kleine Maräne (*Coregonus albula* L.) im Nilakka und Pielavesi. Annales Academiae Scientiarum Fennicae, Serie A, vol. XXI, No. 2, 1924, 134 pp., 24 figs., 2 maps. Helsinki.
- JÄRVI, T. H. 1930. On the fluctuations in abundance exhibited by the stock of lake-herring (*Coregonus albula*) in Lake Keitele, Finland. Rapp. et Procès-Verb., Cons. Perm. Internat. Explor. Mer, vol. LXV, no. 20, 1930, pp. 183-188, 2 figs. Copenhagen.
- JENSEN, AAGE J. C. 1928. The relation between the size of the plaice stock and the quantity of "First Class Plaice Food" in certain parts of the Limfjord. Report, Danish Biol. Sta., Bd. of Agri., vol. XXXIV, 1928, pp. 87-99, 3 figs. Copenhagen.
- JENSEN, AAGE J. C. 1932. The effect of the plaice fishery on the stock of undersized plaice and its influence on the yield of the plaice fishery in the North Sea. Rapp. et Procès-Verb., Cons. Perm. Internat. Explor. Mer, vol. LXXX, no. IV, 1932, pp. 3-6. Copenhagen.
- JOHANSEN, A. C. 1928. The extent of the annual transplantations of plaice in the Limfjord and the yield resulting therefrom. Report, Danish Biol. Sta., Bd. of Agri., 1928, pp. 53-86. Copenhagen.
- JUDAY, C., and EDWARD A. BIRGE. 1930. The highland lake district of northeastern Wisconsin and the Trout Lake limnological laboratory. Trans., Wisconsin Academy of Science, Arts, and Letters, vol. XXV, 1930, pp. 337-352. Madison.
- JUDAY, C., and EDWARD A. BIRGE. 1932. Dissolved oxygen and oxygen consumed in the lake waters of northeastern Wisconsin. Trans., Wisconsin Academy of Science, Arts, and Letters, vol. XXVII, 1932, pp. 415-486, 35 figs. Madison.
- JUDAY, C., and EDWARD SCHNEBERGER. 1930. Growth studies of game fish in Wisconsin lakes. Notes, Biol. Lab., Wisconsin Geol. and Nat. Hist. Sur., March 1930. Madison. [Mimeographed.]
- JUDAY, C., and EDWARD SCHNEBERGER. 1933. Growth studies of game fish in Wisconsin waters—second report. Notes, Limnol. Lab., Wisconsin Geol. and Nat. Hist. Sur., April 1933, 10 pp. Madison. [Mimeographed.]
- KEYS, ANCEL B. 1928. The weight-length relation in fishes. Proc., Nat. Acad. of Science, vol. XIV, no. 12, 1928, pp. 922-925. Washington.
- KOELZ, WALTER N. 1926. Fishing industry of the Great Lakes. Appendix XI, Report, U. S. Comm. Fish., 1925 (1926), pp. 553-617. Washington.
- KOELZ, WALTER N. 1931. The coregonid fishes of northeastern America. Papers, Michigan Academy of Science, Arts, and Letters, vol. XIII, 1930 (1931), pp. 303-432. Ann Arbor.
- KROGIUS, F. 1933. Zur Kenntnis der Systematik und Biologie der Baikal Renken. Travaux de la Station Limnologique du lac Bajkal, vol. V, 1933, pp. 5-154.
- LECHLER, HERMANN. 1929. Untersuchungen über die Reinanke des Mondsees. (I.) Zeitschrift für Fischerei und deren Hilfswissenschaften, Bd. XXVII, Heft 4, 1929, S. 547-560. Neudamm und Berlin.
- LECHLER, HERMANN. 1930. Untersuchungen über die Reinanke des Mondsees. (II.) Zeitschrift für Fischerei und deren Hilfswissenschaften, Bd. XXVIII, 1930, S. 485-493. Neudamm und Berlin.
- LEE, ROSA M. [Mrs. T. L. Williams], and GEORGE T. ATKINSON. 1912. Report on plaice transplantation experiments to various fishing grounds in the North Sea. Marine Biol. Asso. Internat. Invest., Report IV (Cd 6125), 1912, pp. 107-151. London.
- MCCAY, C. M. 1933. Is longevity compatible with optimum growth? Science, N. S., vol. 77, no. 2000, April 28, 1933, pp. 410-411. Lancaster, Pa.
- MCCAY, C. M., A. TUNISON, MARY CROWELL, D. K. TRESSLER, S. P. MACDONALD, JOHN W. TITCOMB, and EBEN W. COBB. 1931. The nutritional requirements of trout and chemical composition of the entire trout body. Trans., American Fish. Soc., vol. 61, 1931, pp. 58-79. Hartford.

- MOTTLEY, C. McC. 1932. The propagation of trout in the Kamloops district, British Columbia. Trans., American Fish. Soc., vol. 62, 1932, pp. 144-151. Hartford.
- OLOFSSON, OSSIAN. 1932. Sikens tillväxt under en varm och en kall sommar. Ny Svensk Fiskeritidskrift, Nr. 14, 1932, S. 163-166. Goteborg.
- OSBORNE, THOMAS B., LAFAYETTE B. MENDEL, and EDNA L. FERRY. 1917. The effect of retardation of growth upon the breeding period and duration of life of rats. Science, N. S., vol. 45, no. 1160, March 23, 1917, pp. 294-295. New York.
- PIROGNIKOFF, P. L. 1927. Materials concerning age and growth rate of rudd (*Rutilus rut. lacustris* Pallas) from the Lake Chani. Reports, Ichthyological Laboratory, Siberia, vol. II, no. 5, 1927, pp. 3-15. Krasnoyarsk.
- PRITCHARD, ANDREW L. 1928. A preliminary study of the genus *Leucichthys* in the Canadian waters of Lake Ontario. University of Toronto Studies, Publications, Ontario Fish. Res. Lab., no. 32, 1928, pp. 7-25. Toronto.
- PRITCHARD, ANDREW L. 1931. Taxonomic and life history studies of the ciscoes of Lake Ontario. University of Toronto Studies, Publications, Ontario Fish. Res. Lab., no. 41, 1931, pp. 5-78. Toronto.
- REIBISCH, J. 1908. Ein Dickenkoeffizient als Mass für Alter und Ernährungszustand der Fische. Die Beteiligung Deutschlands an der internationalen Meeresforschung, Jahresbericht IV/V, 1908, S. 59-65. Berlin.
- REIBISCH, J. 1911. Biologische Untersuchungen über Gedeihen, Wanderung und Ort der Entstehung der Scholle (*Pleuronectes platessa*) in der Ostsee. Wissenschaftliche Meeresuntersuchungen, herausg. von der Kommission zur Untersuchung der deutschen Meere, neue Folge, Bd. XIII, Abteilung Kiel, Nr. 18, 1911, S. 127-204, 11 figs., 28 tables. Kiel und Leipzig.
- RICH, WILLIS H. 1926. Progress in biological inquiries 1925. Appendix I, Report, U. S. Comm. Fish., 1926 (1927), pp. 1-36. Washington.
- RUGDE. 1923. Some notes from Norway. Salmon and Trout Magazine, No. 34, 1923, pp. 333-337. London.
- RUSSELL, E. S. 1932. Is the destruction of undersized fish by trawling prejudicial to the stock? Rapp. et Procès-Verb., Cons. Perm. Internat. Explor. Mer, vol. LXXX, no. 8, 1932, pp. 2-13, 1 fig. Copenhagen.
- SCHULTZ, LEONARD P. 1933. The age and growth of *Atherinops affinis oregonia* Jordan and Snyder and of other subspecies of bay smelt along the Pacific coast of the United States. University of Washington Publications in Biology, vol. 2, no. 3, 1933, pp. 45-102. Seattle.
- SCOTT, WILL. 1931. The lakes of northeastern Indiana. Investigations of Indiana Lakes, No. 3. Department of Conservation, Division of Fish and Game, Indiana, Publication No. 107, 1931, pp. 61-145. Indianapolis.
- SEGERSTRÅLE, CURT. 1932. Über die jährlichen Zuwachszonen der Schuppen und Beziehungen zwischen Sommertemperatur und Zuwachs bei *Abramis brama* sowie einigen anderen Cypriniden in Süd-Finland, 1911-1930. Acta Zoologica Fennica, vol. 13, 1932, 42 pp. Helsinki.
- SEGERSTRÅLE, CURT. 1933. Über scalimetrische Methoden zur Bestimmung des linearen Wachstums bei Fischen, insbesondere bei *Leuciscus idus* L., *Abramis brama* L., und *Perca fluviatilis* L. Acta Zoologica Fennica, vol. 15, 1933, pp. 1-168, 37 figs. Helsinki.
- STORROW, B. 1932. Concerning fluctuations in marine food fishes. Jour., Animal Ecology, vol. 1, no. 2, 1932, pp. 160-165. Cambridge.
- STRODTMANN, S. and H. LANGHAMMER. 1925. Untersuchungen über die Scholle in der westlichen Ostsee. Berichte der deutschen wissenschaftlichen Kommission für Meeresforschung, N. F., Bd. I, Nr. xi, 1925, S. 305. Berlin.
- SURBECK, G. 1921. Beitrag zur Kenntniss der schweizerischen Coregonen. Schweizerische Fischerei-Zeitung, Jahrgang 29, Nr. 3, 1921, S. 52-59. Bern.
- TESTER, ALBERT L. 1932. Rate of growth of the small-mouthed black bass (*Micropterus dolomieu*) in some Ontario waters. University of Toronto Studies, Publications, Ontario Fish. Res. Lab., no. 47, 1932, pp. 207-221. Toronto.
- THOMPSON, D'ARCY WENTWORTH. 1917. On growth and form. 793 pp., 1917. Cambridge University Press. Cambridge.
- THWAITES, F. T. 1929. Glacial geology of part of Vilas County, Wisconsin. Trans., Wisconsin Academy of Science, Arts, and Letters, vol. XXIV, 1929, pp. 109-125. Madison.

- TITCOMB, JOHN W., EBEN W. COBB, MARY F. CROWELL, and C. M. MCCAY. 1928. The nutritional requirements and growth rates of brook trout. *Trans., American Fish. Soc.*, vol. 58, 1928, pp. 205-231, 9 charts. Hartford.
- TJURIN, P. V. 1927. About the relation between the length of the fish and its weight. *Reports, Ichthyological Lab., Siberia*, vol. II, no. 3, 1927, pp. 3-21. Krasnoyarsk.
- VAN OOSTEN, JOHN. 1923. The whitefishes (*Coregonus clupeaformis*). A study of the scales of whitefishes of known ages. *Zoologica*, vol. II, no. 17, June 19, 1923, pp. 380-412, figs. 137-144, tables I-VII. New York.
- VAN OOSTEN, JOHN. 1929a. Some fisheries problems on the Great Lakes. *Trans., American Fish. Soc.*, vol. 59, 1929, pp. 63-85. Hartford.
- VAN OOSTEN, JOHN. 1929b. Life history of the lake herring (*Leucichthys artedii* Le Sueur) of Lake Huron as revealed by its scales, with a critique of the scale method. *Bull. U. S. Bur. Fish.*, vol. XLIV, 1928 (1929), pp. 265-428, 43 figs. Washington.
- VAN OOSTEN, JOHN. 1933. Preliminary report on investigation of chub net meshes in Lake Michigan. *The Fisherman*, vol. 2, no. 4, March 1933, pp. 3-4, 8. Grand Haven.
- WAGLER, ERICH. 1927. Die Blaufelchen des Bodensees (*Coregonus wartmanni* Bloch). *Internationale Revue der gesamten Hydrobiologie und Hydrographie*, Bd. 18, Nr. 3/4, 1927, S. 129-230, 13 figs., 11 plates. Leipzig.
- WAGLER, ERICH. 1930a. Die Coregonen in den Seen des Voralpengebietes. II. Die Schwebrenke des Tegernsees. *Archiv für Hydrobiologie*, Bd. 21, Heft 3, 1930, S. 455-469. Berlin.
- WAGLER, ERICH. 1930b. Die Coregonen in den Seen des Voralpengebietes. III. Die Schwebrenke des Ammersees. *Archiv für Hydrobiologie*, Bd. 21, Heft 3, 1930, S. 470-482. Berlin.
- WAGLER, ERICH. 1932. Die Coregonen in den Seen des Voralpengebietes. V. Der Silberfelchen des Untersees. *Internationale Revue der gesamten Hydrobiologie und Hydrographie*, Bd. 26, Nr. 3/4, 1932, S. 195-222, 7 figs. Leipzig.
- WAGLER, ERICH. 1934. Die Coregonen in den Seen des Voralpengebietes. VII. Der Kilch des Bodensees (*Coregonus acronius* von Rapp). *Internationale Revue der gesamten Hydrobiologie und Hydrographie*, Bd. 30, Nr. 1/2, 1934, S. 1-48, 8 figs. Leipzig.
- WALFORD, LIONEL A. 1932. The California barracuda (*Sphyræna argentea*). I. Life history of the California barracuda. II. A bibliography of barracudas (*Sphyrænidae*). *Division of Fish and Game of California*, Fish Bull. No. 37, 1932, pp. 7-120. Sacramento.
- WEATHER BUREAU, U. S. DEPARTMENT OF AGRICULTURE. 1923-1931. Climatological Data for the United States. Vols. X-XVIII, 1923-1931. Washington.
- WEYMOUTH, FRANK W. 1918. Contributions to the life history of the Pacific Coast edible crab (*Cancer magister*). (No. 3.) Report, Comm. Fish., 1917 (1918), Province of British Columbia, pp. Q 81-Q 90, 2 figs. Victoria.
- WEYMOUTH, FRANK. 1923. The life history and growth of the Pismo clam (*Tivela stultorum* Mawe). *State of California Fish and Game Commission*, Fish Bulletin No. 7, 1923, pp. 5-120, 15 figs., 18 graphs. Sacramento.
- WILLER, ALFRED. 1924. Die kleine Maräne (*Coregonus albula* L.) in Ostpreussen. *Internationale Revue der gesamten Hydrobiologie und Hydrographie*, Bd. XII, Heft 3/4, 1924, S. 248-265. Leipzig.
- WILLER, ALFRED. 1926. Untersuchungen über den Stint (*Osmerus eperlanus* L.) in Ostpreussen. *Zeitschrift für Fischerei, und deren Hilfswissenschaften* Bd. XXIV, Heft 4, 1926, S. 521-558. Neudamm-Berlin.
- WILLER, ALFRED. 1929. Untersuchungen über das Wachstum von Fischen. *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie*, Bd. IV 1929, S. 668-684. Rome.
- WRIGHT, STILLMAN. 1929. A preliminary report on the growth of the rock bass, *Ambloplites rupestris* (Rafinesque), in two lakes of northern Wisconsin. *Trans., Wisconsin Academy of Science, Arts, and Letters*, vol. XXIV, 1929, pp. 581-595. Madison.
- ZABINSKI, JAN. 1929. The growth of black beetles and of cockroaches on artificial and on incomplete diets. *British Jour. Exper. Biol.*, vol. VI, no. 4, 1928, pp. 360-385. Edinburgh.

APPENDIX A. GROWTH OF THE CISCO IN ALLEQUASH AND TOMAHAWK LAKES

Small collections of ciscoes were obtained from Allequash Lake in 1928 and in 1930 and from Tomahawk Lake in 1928. Since it is unlikely that any further collections of ciscoes will be made in either of these lakes in the near future, the available growth data for each of the populations are being presented at this time.

Tables 1 and 2 show the average length, average weight, average value of K , and the calculated length at the end of each year of life in each age group for each of the three collections. The most noteworthy features of the growth in these two populations are the slow growth during the first year of life in the Allequash fish, the generally excellent growth of the Tomahawk Lake cisco, and the indication that in the Allequash Lake cisco the year 1929 was one above the average in the amount of growth. (It should be pointed out that 1929 was a good growth year in the Trout Lake, Muskellunge Lake, and Silver Lake cisco populations.) The I group of the 1930 Allequash collection shows a particularly high growth for the 1929 season. It is, of course, true that the selective action of gear would be expected to cause a too high calculated growth for this group in any year but selection can hardly explain such a great growth as that which is present here in 1929, for it may be seen that in 1929 the calculated growth for the first year of life is 29 millimeters greater than that calculated for 1927 from the 1928 I group.

TABLE 1.—*Allequash Lake cisco*

[Length, weight, value of K , and calculated length at the end of each year of life. Division of data is according to year class and year of capture. Sexes combined]

Year class	Year of capture	Age	Number of specimens	Weight in grams	K	Length in millimeters	Year of life			
							1	2	3	4
1925	1928	III	3	54	1.50	155	54	101	127	-----
1926	1928	II	17	45	1.51	144	59	107	-----	-----
	1930	IV	1	140	1.67	203	49	98	138	175
1927	1928	I	27	25	1.36	123	64	-----	-----	-----
	1930	III	12	108	1.56	190	58	115	165	-----
1928	1930	II	11	71	1.54	167	54	133	-----	-----
1929	1930	I	42	42	1.43	143	93	-----	-----	-----

TABLE 2.—*Tomahawk Lake cisco, 1928*

[Length, weight, value of K , and calculated length at the end of each year of life for each age group. Sexes combined]

Year class	Age	Number of specimens	Weight in grams	K	Length in millimeters	Year of life				
						1	2	3	4	5
1923	V	1	156	1.53	217	81	138	172	193	210
1924	IV	16	146	1.59	209	78	141	174	198	-----
1925	III	39	125	1.58	199	76	140	182	-----	-----
1926	II	11	99	1.61	183	81	155	-----	-----	-----
1927	I	1	35	1.42	135	83	-----	-----	-----	-----

Because of the poor growth in the first year of life the general growth of the Allequash Lake cisco differs from that of all four populations considered in the main body of this study. The closest resemblance is probably with the Silver Lake cisco. The growth of the Tomahawk Lake cisco although poorer than that of the Clear Lake cisco is distinctly better than that found in Trout, Muskellunge, and Silver Lakes.

In both Allequash and Tomahawk Lakes the high values of K indicate good condition.

The exceptional conditions under which the Allequash cisco lives should be mentioned. (See table 1 of general paper.) Formerly there existed a rather general belief that the coregonids as a stenothermic form adapted to a cold-water habitat were limited in their distribution to the larger, deeper, lakes. Willer (1924) showed that such a generalization did not apply to the distribution of the kleine Maräne, *Coregonus albula*, in the lakes of East Prussia. Scott (1931) called attention to the exceptional conditions under which the cisco lives in Indian Village Lake (Indiana). This lake is small and shallow (6.4 meters) and in midsummer there is "only a trace" of oxygen below 4 meters. Allequash Lake is another example of a shallow-water habitat for the cisco. The cisco here must not only adjust itself to a wide annual range of temperature variation but also to unusual associates in the form of other species of fish. Along with the 70 ciscoes captured in 1930 were taken 1 blue gill, 15 suckers, 22 pike-perch, 32 rock bass, and 182 perch.

THE PROGRESSIVE FISH CULTURIST

NEWS AND VIEWS FROM MANY SOURCES ON PRACTICAL HATCHERY PROBLEMS

ISSUED BY THE
BUREAU OF FISHERIES, U. S. DEPARTMENT OF COMMERCE

Memorandum I-131

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No. 23.

AGE DETERMINATION OF FISH FROM SCALES ; METHOD AND APPLICATION TO FISH CULTURAL PROBLEMS

By Ralph Hile, Ph.D.
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U. S. Bureau of Fisheries

METHOD OF AGE DETERMINATION

THE SCIENCE of "scale reading", or determination of the age of fish from the examination of their scales, is less than 40 years old. Yet today the publications on the subject are to be numbered by the hundreds, and there is scarcely any phase of fish and fishery work that has not been benefited by this powerful tool for investigation. Fish culture is no exception to this rule. It is because of the increasing interest of fish culturists in scale reading and their numerous requests for information on the subject, that I have been asked to prepare a brief discussion of the method of age determination in fishes.

The determination of the age of fish from their scales is based on the interpretation of the microscopic structures appearing on the surface of the scale. The nature of these structures can be brought out best by reference to the accompanying facsimile drawings of scales of the two most common types. The scale of figure 1, taken from a Lake Huron herring, is of the cycloid type. Among the fish

with this type of scale are the whitefish, trout, salmon, and muskellunge. The other scale, figure 2, which is that of a Lake Erie yellow pike-perch (or wall-eyed pike) is of the ctenoid type. The term "ctenoid" refers to the ctenii or small teeth that appear on the posterior portion of the scale. Other fish with ctenoid scales are perch, black bass, bluegill, or sunfishes. Each of these scales occupies the position it would have on the fish if the fish's head were pointed toward the top of the page. The forward part (top in the pictures) is imbedded in the fish's skin and is covered by the hinder portion of the preceding scales. The hinder part is exposed and is the part visible when the scale is on the fish.

It will be noticed that, with the exception of the toothed area on the pike-perch scale, each scale is covered with roughly concentric lines or ridges known as circuli. The distribution of these lines is not perfectly regular but shows breaks at varying intervals. These breaks are the year marks or annuli by which age is determined. The herring scale has three annuli, i. e., the fish had lived three full years and was in its fourth year when it was caught. The pike-perch scale has one annulus, and the fish was therefore in its second year of life when it was captured.

At the end of the summer season the growth of the fish slows down and during the winter ceases entirely or nearly so. Since the scale grows along with the fish, scale growth also comes to a standstill. When body and scale growth are resumed in the spring the first circuli of the new year are laid down without any reference to the position of the last circuli of the preceding summer. The result is a break in the regularity of the circuli -- the year mark or annulus. An outstanding feature of the year mark may be noticed at the sides of the scale particularly toward the hinder end. The last circuli of the summer do not pass completely around the scale but come to an end toward the back of the scale. The circuli of the next spring do, on the contrary, pass entirely around the scale and thus cut across the ends of those of the preceding year.

A further aid in the detection of the annulus is the broken and irregular distribution of the circuli in the region of the year mark. It is also fairly common for the scale to have a darker appearance in the neighborhood of the annulus. This dark area results from the fact that with the slowing down of growth in the fall the circuli are laid down more closely together than in periods of rapid growth. However, dark bands are not always present near the annulus, and, on the other hand, they may occur in the summer growth area. Consequently, the determination of age based entirely on counting dark bands does not give reliable results.

The presence of accessory checks or false annuli within the summer growth area often adds greatly to the difficulties of scale reading. These summer checks may usually be detected because of their location with respect to the true annuli, their characteristic faintness, and the variation in their strength from one scale to another. Fortunately the markings of scales with accessory checks usually

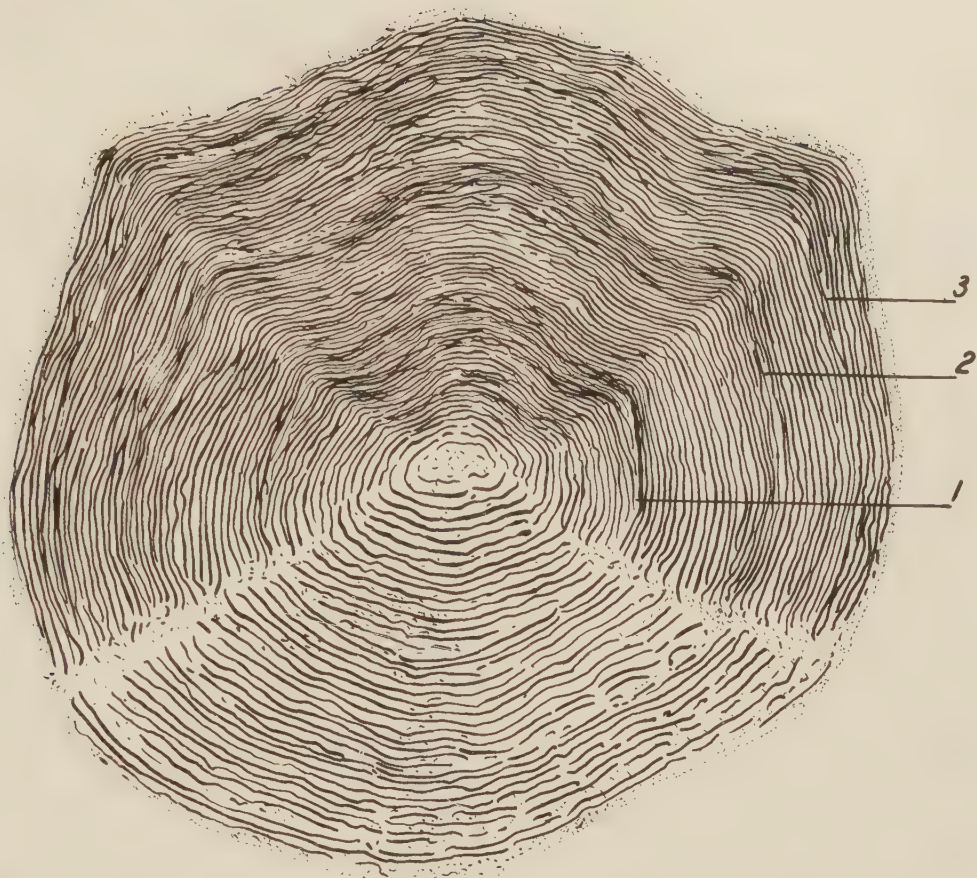


FIG. 1 SCALE OF LAKE HURON HERRING IN ITS FOURTH YEAR OF LIFE (AGE-GROUP III).

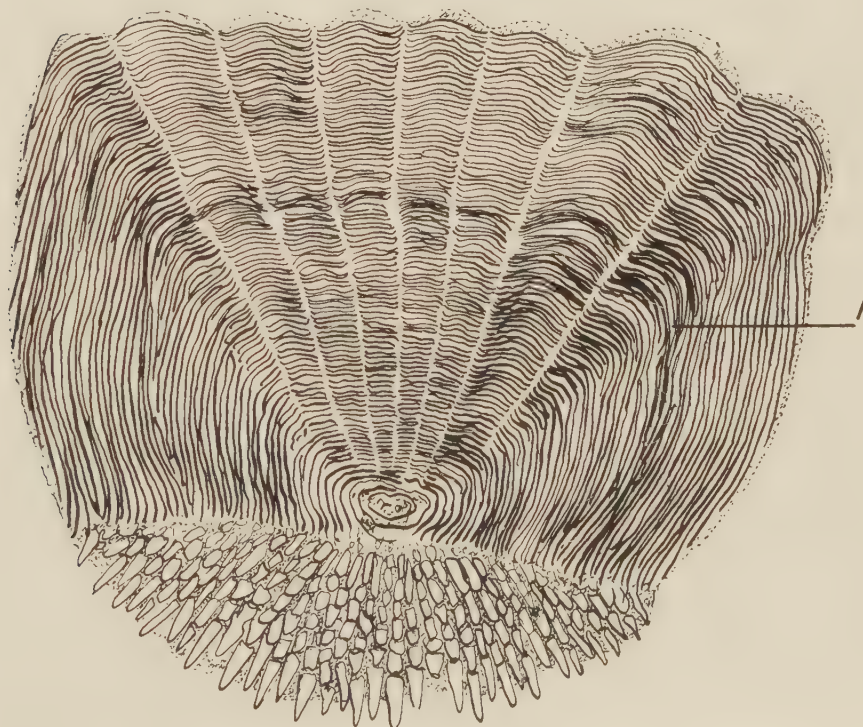


FIG. 2 SCALE OF LAKE ERIE YELLOW PIKE-PERCH IN ITS SECOND YEAR OF LIFE (AGE-GROUP I).

have a typical confused appearance that puts the investigator on his guard. In practice even the experienced worker will have to discard about 5 percent of his scales as wholly unreadable. The inexperienced reader should probably not attempt to determine ages on as many as 95 percent of his fish, but should confine his early readings at least to the most clearly marked scales.

The ease with which scales can be read varies not only with the species but also between different populations of the same species and between different individuals of the same population. For example, well experienced investigators have declined entirely to attempt to read the scales of the common sucker of Lake Erie, and a Norwegian author has reported that only 30-40 percent of the scales of the cod yield reliable age determinations. Even in species whose scales are ordinarily easily read it may be difficult or impossible to make reliable age determinations in exceptionally slow growing populations. In any population of any species the determination of age in very large and very old individuals may be difficult because of the thickness of the scale and because of the crowding of the annuli in the later years of slow growth. Thus it may be seen that the question of the feasibility of scale reading is a separate problem for each species, each population, and even for each individual fish. Consequently, the utmost care and caution must be exercised at all times to insure the greatest accuracy of results. An inexperienced worker should not attempt extensive scale readings without having the accuracy of his age determinations verified by a trained investigator.

If very large numbers of scales are to be read, it is desirable to have available special optical equipment for the projection of the scale image on a screen. It is possible, nevertheless, to read all but the largest and thickest scales by means of a binocular or a compound microscope. If a microscope is used, it should be equipped with a 48 mm. objective. The best procedure consists of soaking the scales in water, cleaning them of slime and dirt, and examining them immersed in water.

The following suggestions are offered in connection with the collection of scales. The best scales are usually those from the mid-region of the body, immediately above or below the lateral line. However, scales from the lateral line itself should be avoided. Before the scale sample is removed the slime should be scraped off the area from which the scales are to be taken. Otherwise this slime will dry on the scales and make them very difficult to clean. Each sample of 8 or 10 scales should be stored in a small envelope on which all data for the individual fish are recorded. Ordinarily it is not necessary to examine more than 2 or 3 of the scales in detail, but a larger number makes possible a more reliable reading of difficult scales and makes allowance for the presence of regenerated scales. These regenerated scales are those formed to take the place of scales that have been lost from the fish. They are characterized by a clear central area and are obviously worthless for purposes of age determination.

APPLICATIONS OF AGE DETERMINATIONS IN FISH CULTURE

Age determinations may be of great value in fish culture, particularly in the selection of brood stock, and in the formation of stocking policies and programs.

Hatchery brood fish are frequently obtained from natural waters. When this procedure is employed, it is advisable to take the breeders from a population that shows a good rate of growth. Rapid growth indicates favorable environmental conditions, and fish taken from good natural waters may be expected to be healthier and more virile than those taken from poor waters where growth is slow. There is also the possibility that differences in the growth rates of natural populations may be, to a certain extent, hereditary. Certainly it would be highly desirable to have brood fish whose offspring will have the greatest possible inherent capacity for growth.

The knowledge of growth rates based on age determinations is probably of greatest value to fish culturists in connection with the formation of stocking policies. In the early history of fish culture in this country attention was given almost exclusively to the development of the most efficient methods of producing fry and fingerlings, but little consideration was given the question of the suitability of the waters in which these young fish were planted. As a result, untold quantities of fish were planted in waters where they could not possibly survive or where they could not prosper even if they did manage to remain alive. Within more recent years, however, this wastage that results from haphazard planting is being corrected more and more by surveys conducted to determine the suitability of waters for the different species of fish that might be planted in them. The effectiveness of such surveys can be increased greatly if the determination of the growth rates of the natural populations of fish is included as an integral part of the method. Not always is it desirable to plant young of a certain species in streams or lakes merely because these waters possess physico-chemical and biological characteristics that are favorable for the species in question. It is altogether possible, and very frequently true, that the fish are already so abundant that they do not enjoy normal growth, and that artificial additions to their numbers would only make a bad condition worse.

It is quite probable that with continued experience it may be possible to employ periodic age-determinations as one of the sources of data for following changes over a period of years in the abundance of fish in important waters. If the changes in the abundance of fish are known the stocking program can be adjusted accordingly. When the growth rate falls off, the fish are too abundant, and plantings should be reduced or suspended. On the other hand, if the rate of growth increases, it may be considered advisable to increase the number of fish planted. By this means each stream or lake so "managed" would have its population held near its optimum density.

Mention should be made also of the fact that a knowledge of the rate of growth of a given species in a certain body of water may be used to estimate the time at which newly planted fish will be large enough to be caught, and thus serve as a valuable check on the results of these plantings.

Low Production May Not Mean Depletion

Statistics of Total Catch Cannot Be Taken As a Reliable Basis For Judging Changes in the Condition of a Fishery; Must Consider Fishing Intensity

By RALPH HILE, U. S. Bureau of Fisheries

In past years we have been almost completely dependent on tabulations of the total catch in different calendar years for the estimation of the condition of the fisheries for the various Great Lakes species. A large catch has generally been taken to indicate that fish are abundant and a small catch to show that the abundance of fish is relatively low. It has been realized, of course, that changes in the extent of fishing operations have an effect on the total catch for the year, but in the absence of data on fishing intensity, this possible effect has had to occupy the position of an unknown quantity. As an illustration of the nature of the statistical data available in past years and of the type of conclusions that were naturally drawn from them, consider the following tabulation of the catch of chubs in small mesh gill nets in Lake Michigan on the eastern shore between Cathed Point and Arcadia over the six-year period, 1929-1934. The catches of the different years are expressed also as percentages of the average annual production of 92,094 pounds for the six-year period. Frankfort is the leading port in the chub fishery of the area.

Year	Catch of Chubs (Pounds)	Percentage of Average
1929	227,708	247
1930	113,668	123
1931	49,550	54
1932	49,324	54
1933	31,223	34
1934	81,091	88
Average	92,094	100

It may be seen at once that the production of chubs in the Frankfort area of Lake Michigan underwent a rapid decline following 1929. The production of 1930 was only half that of 1929, and the approximately equal productions of 1931 and 1932 were less than half the 1930 production, or less than one fourth the 1929 production. In 1933 the catch

of chubs fell still further to a low point of 31 thousand pounds, or less than one seventh of the 1929 yield. The 1934 catch was 50,000 pounds greater than that of 1933, but was still 12 per cent below the six-year average of 92 thousand pounds.

Unquestionably these figures present an alarming picture. Such a rapid decline in production as that which occurred from 1929 to 1933 points toward a possibly disastrous reduction in the abundance of chubs in the area. Even the 1934 increase offers little consolation since the 81 thousand pound yield of that year was only a little more than a third of the 1929 catch. Consequently, it would appear reasonable to conclude that the chub stock of the region stands in serious danger of depletion, and that restrictive measures should be imposed on the fishery in order to save it from possible ruin.

Fortunately, the data made available by the reports of daily fishing activity submitted at the end of each month to the Michigan Department of Conservation by all commercial fishermen of the state make it possible to show that the above conclusion based on statistics of total production is almost entirely invalid. In spite of the decrease in production that occurred, the actual abundance of chubs in the Frankfort area of Lake Michigan fluctuated within rather narrow limits over the six-year period, 1929-1934, and there is little or nothing to indicate a serious depletion of the stock within this period. These facts appear from the following tabulation of the average catch in pounds of chubs per lift of 25 thousand feet of chub nets for each of the six years, 1929-1934. The average for each year is presented also as a percentage of the six-year average lift of 540 pounds of chubs per 25 thousand foot gang.

Continued on Page Two

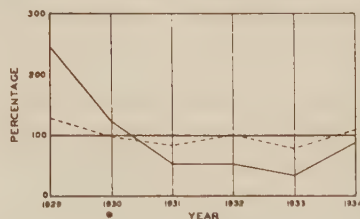
Low Production May Not Mean Depletion

Continued from Page One

Year	Average Lift of Chubs per Gang of 25,000 Ft.	Percentage of 6-Year Average
1929	698	129
1930	530	98
1931	455	84
1932	542	100
1933	428	79
1934	588	109
Average	540	100

The above data demonstrate that the abundance of chubs in the Frankfort region of Lake Michigan, measured in terms of the lift per gang of 25 thousand feet, showed a relatively limited variation in the six-year period, 1929-1934. The year of the greatest abundance of chubs (1929) was only 29 per cent above the six-year average, and the year of least abundance (1933) was only 21 per cent below the six-year average. These fluctuations in abundance are certainly no greater than those that ordinarily occur in any fishery. They offer no cause for fear concerning the welfare of the chub fishery in the Frankfort region.

The accompanying graph, which shows the percentage deviations from the six year average of both the production (solid line) and the abundance (broken line) of chubs in the area brings out in a striking manner how misleading the record of total production may be if there is not available at the same time a record of the amount of the fishing effort that led to the recorded production.



Production of chubs (solid line) and abundance of chubs (broken line) in the Frankfort area of Lake Michigan, 1929-34, expressed as percentages of the six-year average.

From the graph it may be seen that in 1929 the production of chubs was 247 per cent of the six-year average (100 per cent), but at the same time the abundance of chubs was only 129 per cent. In 1930 the production dropped from 247 to 123 per cent,

while abundance dropped from 129 to 98 or two per cent below average. The 1930 production showed another big drop, this time to the low level of 54 per cent of the average, but the abundance dropped only 14 per cent (from 98 to 84 per cent of average.) The abundance of chubs in 1932 equalled the 1929-1934 average exactly, but nevertheless the 1932 production was only 54 per cent of average. The year 1933 was the poorest of the six with respect both to production and abundance of chubs. However, even in this poor year, with a production of only 34 per cent of average, the abundance of chubs was still 79 per cent of average. Both production and abundance increased in 1934, in which year production reached a point only 12 per cent below average and abundance rose to nine per cent above average. (The increase in catch per gang in 1934 may have been due in part to a decrease in the size of the mesh in commercial gear.)

Attention should be called to the fact that, in general, years that show a decrease in abundance will also show a decrease in production and that an increase in abundance is accompanied by an increase in production. This relationship depends on the fact that fishermen fish more nets in good years than in bad. Nevertheless, the tremendous fluctuations in production as compared with the relatively small fluctuations in abundance demonstrates conclusively that in this fishery, changes from year to year in production depended primarily on changes in the amount of twine fished rather than on changes in the abundance of chubs on the grounds.

It may be concluded, therefore, that statistics of total catch can not be taken as a reliable basis for judging changes in the condition of a fishery. It is necessary to have also statistics of fishing intensity. These essential data on the extent of fishing operations can be obtained only from the daily records of fishing operations of individual fishermen. In the interests of sound fishery regulation, fishermen residing in states with a daily report system should endeavor to submit only complete and accurate reports, while fishermen in states without such a system should encourage and cooperate whole-heartedly with any movement toward the establishment of this valuable and reliable method of collecting commercial fisheries statistics.

SUMMARY OF INVESTIGATIONS ON THE MORPHOMETRY OF THE CISCO, *LEUCICHTHYS* *ARTEDI* (LE SUEUR), IN THE LAKES OF THE NORTHEAST- ERN HIGHLANDS, WISCONSIN *

RALPH HILE

INTRODUCTION

THE morphometric studies on the cisco or lake herring, *Leucichthys artedi* (Le Sueur), which will be summarized briefly in this paper are part of a program of investigation of the fishes of the lakes in the northeastern highland district, Wisconsin, conducted coöperatively by the Wisconsin Geological and Natural History Survey and the United States Bureau of Fisheries. For the morphometric studies 1,548 specimens were employed, all of them collected in the summers of 1931 and 1932 from four "type" lakes, selected on the basis of their size, depth, and physicochemical and biological characteristics. Of this number 753 individuals were used to determine the general nature of the morphological variations in the Trout Lake, Muskellunge Lake, Silver Lake, and Clear Lake cisco populations, while 795, collected from Muskellunge Lake in 1932, were employed in a detailed examination of certain morphological differences between the 1928 and 1929 year classes of that population. Limitations of space necessitate the omission of many interesting facts brought out by the rather voluminous data. An attempt will be made, however, to present in this paper all the more important conclusions, together with a small amount of illustrative material. A complete presentation of the material will be published elsewhere.

Of the four populations studied, three (those from Muskellunge Lake, Silver Lake, and Clear Lake) were assigned by Koelz (1931) to the subspecies *clarensis*. The cisco population of Trout Lake was

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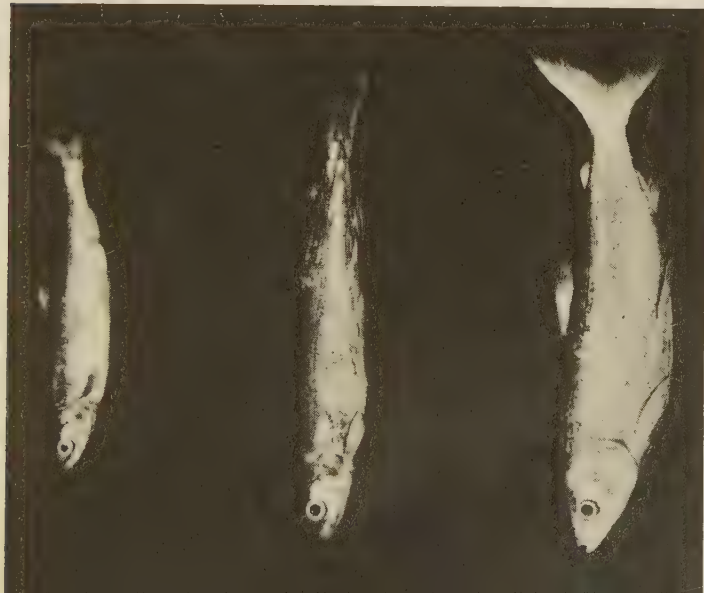
included by the same author under the subspecies *clemensi*. Clear Lake is the type locality for *clarensis*.

The purposes of the morphometric studies were the determination of: (1) the range of variation of morphometric characters within single cisco populations; (2) the extent of morphological differences between populations of the same and of different subspecies; and (3) the extent of morphological differences between populations and between year classes of a single population, traceable to the direct modifying effects of the environment. Under (1) may be included the questions of sex differences and of the change of body proportions with growth. The third purpose listed includes the important problem of the relationship between growth rate and body form. Extensive data on the growth histories of each of the four cisco populations are available from my studies on the growth of these fish (Hile, MS). Further, the individual growth history of each of the 753 individuals employed in the general morphometric survey was determined from the assessment of age and the calculation of past growth, based on scale examinations and measurements.

RANGE OF VARIATION

Table I shows the mean value for each cisco population for each of the morphometric characters included in the study. In the same table may be found the total range in the value of each morphometric character for each of the subspecies, *clemensi* (Trout Lake) and *clarensis* (Muskellunge, Silver, and Clear lakes). The data of the table show that the four populations exhibit large differences with respect to most of the characters considered. These differences are sufficiently great to indicate that each population must be considered morphologically distinct. Likenesses between any two populations with respect to one character are offset by differences with respect to other characters. It should be pointed out further that, on the whole, the Muskellunge Lake and the Silver Lake populations, assigned by Koelz (1931) to the subspecies *clarensis*, resemble the Trout Lake population, assigned by the same author to the subspecies *clemensi*, more closely than they resemble the population from the *clarensis* type locality, Clear Lake (Pl. LXII, Figs. 1-2). A comparison of the morphological characters of the three *clarensis* populations of this study (Table I) with Koelz' (1931) key to the subspecies of *artedi* shows that these three populations, assigned

PLATE LXII



g. 1. Typical specimens of the cisco:
 (a) from Trout Lake (length, 122 mm.)
 (b) from Muskellunge Lake (length, 152 mm.)
 (c) from Silver Lake (length, 171 mm.)

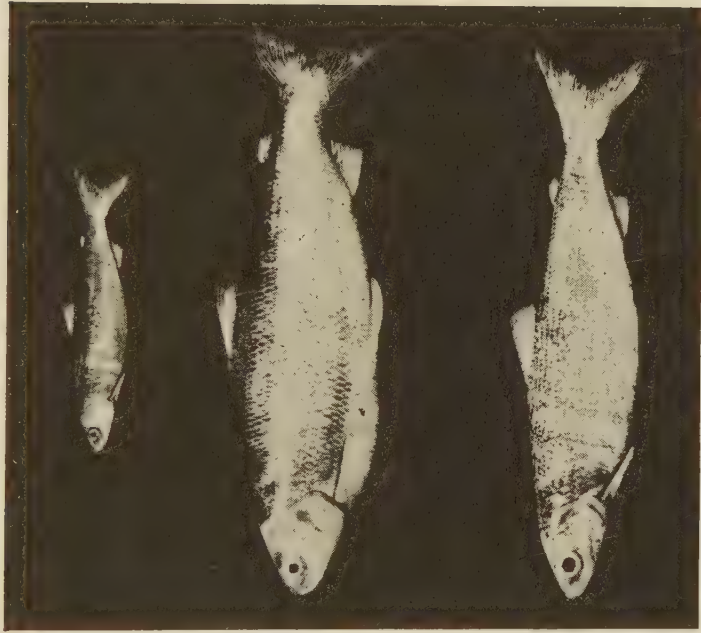


FIG. 2. Typical specimens of the Clear Lake cisco:
 (a) juvenile (length, 167 mm.)
 (b) adult (length, 326 mm.)
 (c) the juvenile, a, to a larger scale



FIG. 3. Comparison of the typical appearance of the heads of the Muskellunge Lake cisco in individuals of the 1929 year class (at left) and the 1928 year class (at right)

TABLE I

AVERAGE VALUE OF MORPHOMETRIC CHARACTERS FOR EACH OF THE FOUR CISCO POPULATIONS; TOTAL RANGE OF VARIATION FOR EACH CHARACTER IN THE SUBSPECIES *CLEMENSI* (TROUT LAKE) AND *CLARENSIS* (MUSKEL-LUNGE LAKE, SILVER LAKE, AND CLEAR LAKE)

Abbreviations: L = standard length; H = head length; D = greatest body depth; W = greatest body width; AT = adipose to caudal distance; DCP = least depth of the caudal peduncle; DB, AN = dorsal and anal fin bases; AD = length of adipose fin; PV = pectoral-ventral distance; E = antero-posterior eye diameter; AV = anal-ventral distance; S = length of snout; M = length of maxillary; P, V = length of pectoral and of ventral fins; DH = height of dorsal fin; R = gill rakers on first arch; Sc = lateral line scales; RD = scale rows above lateral line; RC = scale rows about the peduncle; BR = branchiostegal rays; DR, AR, PR, VR = dorsal, anal, pectoral, and ventral fin rays.

Character	Mean for population				Range for subspecies	
	Trout	Muskel-lunge	Silver	Clear	<i>clemensi</i>	<i>clarensis</i>
L/H *	3.85	4.19	4.38	4.49	3.43- 4.21	3.55- 5.21
L/D	4.27	4.72	4.39	3.66	3.62- 4.90	2.84- 5.69
L/W *	9.17	8.97	8.52	6.65	6.82-12.71	4.43-11.79
L/AT	8.32	8.02	7.67	8.40	6.50-12.45	6.55-10.65
L/DCP	12.67	14.15	13.49	11.54	10.62-16.17	8.88-15.91
L/DB	9.77	9.87	9.53	8.29	7.10-11.73	6.98-12.57
L/AN	9.24	10.00	9.43	9.30	6.86-10.86	7.85-12.43
L/AD	14.43	13.92	13.51	14.29	11.17-18.25	10.65-20.62
L/PV	3.53	3.58	3.40	3.23	3.08- 4.13	2.82- 4.13
L/E *	14.76	15.43	18.39	21.19	10.31-18.00	12.54-27.27
PV/AV	1.13	1.14	1.19	1.14	0.92- 1.35	0.94- 1.40
H/S	4.15	4.38	4.15	4.48	3.50- 5.00	3.42- 5.57
H/E	3.83	3.68	4.17	4.73	3.18- 4.80	2.92- 5.91
H/M *	2.94	3.16	3.11	3.42	2.44- 3.25	2.73- 3.94
D/E	3.46	3.30	4.19	5.86	2.62- 4.70	2.58- 8.45
PV/P *						
male	1.65	1.82	1.82	2.05	1.42- 1.89	1.55- 2.39
female	1.71	1.87	1.96	2.16	1.37- 2.00	1.63- 2.57
AV/V *						
male	1.49	1.66	1.59	1.87	1.23- 1.92	1.38- 2.19
female	1.51	1.70	1.67	1.95	1.26- 1.77	1.37- 2.31
DH/DB *	1.76	1.54	1.54	1.31	1.37- 2.15	1.02- 1.87
R	46.6	45.4	45.1	48.4	39.0- 52.0	39.0- 53.0
Sc	72.5	79.5	78.5	77.9	60.0- 88.0	68.0- 86.0
RD	7.2	7.6	7.6	8.5	6.0- 8.0	7.5- 9.5
RC	20.8	22.0	21.6	24.3	19.0- 23.0	21.0- 26.0
BR	8.4	8.1	8.6	8.8	7.0- 10.0	7.0- 10.0
DR	12.0	12.1	12.0	11.8	11.0- 13.0	10.0- 13.0
AR	12.1	13.0	13.2	12.4	11.0- 13.0	8.0- 15.0
PR	15.0	15.5	15.6	15.1	13.0- 17.0	12.0- 17.0
VR	12.0	11.9	12.2	12.0	11.0- 14.0	11.0- 14.0
Number of specimens	277	110	210	156	277	476

* Characters correlated with growth rate (see p. 624).

by that author to the same subspecies, exhibit structural differences that are greater than those upon which the separations of many of his subspecies have been based.

The range of variation is very large for most of the characters. The great range in the *clarensis* group depends in part on the combination of three dissimilar populations, but the data for the subspecies *clemensi*, based on the Trout Lake population alone, show how widely certain characters may vary within a single stock. This high degree of variability makes the use of large numbers of specimens necessary to obtain reliable average values for most morphometric characters. It is of interest to note that much of the systematic work that has been done on *L. artedi* was not based on large numbers of specimens. Of the seventeen new subspecies of *artedi* described by Koelz (1931) eleven were based on twenty fish or fewer, and six of these eleven on from five to ten specimens. When it is considered that in the light of intensive study the subspecies *clarensis* and *clemensi*, whose descriptions were based on 46 and 84 specimens respectively, fail to stand apart as clearly distinct groups, much skepticism is aroused concerning the validity of numerous other currently recognized subspecies of *artedi*.

Further doubt is thrown on the validity of the data employed in the current systematics of *L. artedi* by the fact that certain body ratios used as diagnostic characters show distinct tendencies to change with increase in age and size. In each of the four cisco populations the relative lengths of the paired fins were found to increase slightly with growth. Other characters that changed with growth were relative greatest body width, relative greatest body depth, relative depth of the caudal peduncle, and the anteroposterior eye diameter in greatest body depth. However, none of these last-named characters showed the same direction of change for all populations. For example, it may be seen (Table II) that relative body depth decreases with growth in the Muskellunge Lake cisco, changes only slightly in the Trout Lake and the Silver Lake ciscoes, and increases with growth in the Clear Lake cisco. It is obvious that body ratios that show marked change with growth are of limited systematic value, particularly if the change proceeds in different directions in different populations.

The chief weakness in the use, for systematic studies, of characters that change in value with growth lies in the difficulty of making

definite comparisons between any two populations. Average values for single populations have little significance, since they must not only be affected by the selective action of the gear employed in taking the sample, but may also be expected to vary from year to year according to the size and age composition of the population. These difficulties cannot be circumvented by limiting comparisons to fish of the same length. Yet, it is well known that ratios that have been shown by this study to change in value with growth have been used as important characters in the current systematics of *L. artedi*.

TABLE II

CHANGE OF RELATIVE BODY DEPTH, L/D, WITH INCREASE IN AGE IN THE FOUR CISCO POPULATIONS

The figures in parentheses show the number of specimens.

Lake	Age group										
	0	I	II	III	IV	V	VI	VII	VIII	IX	X
Trout	4.98 (17)	...	4.25 (11)	4.24 (44)	4.30 (130)	4.28 (56)	4.25 (10)	4.08 (4)	4.10 (3)	4.17 (2)	...
Muskellunge..	...	...	4.43 (29)	4.82 (81)	...	...	...	...	...	...	...
Silver.....	...	4.64 (14)	4.53 (7)	4.38 (38)	4.35 (67)	4.37 (70)	4.37 (13)	4.69 (1)	...	...	...
Clear..... (male)	...	4.38 (10)	3.79 (15)	3.62 (20)	3.52 (6)	3.60 (9)	3.31 (5)	3.44 (12)	3.52 (1)	...	...
Clear..... (female)	...	4.25 (10)	3.74 (11)	3.58 (20)	3.68 (8)	3.57 (4)	3.22 (5)	3.30 (10)	3.31 (7)	3.35 (2)	3.05 (1)

Sexual dimorphism with respect to the paired fins was found in all populations. These sex differences with respect to the relative length of the fins are more pronounced in the pectoral fins than in the ventral fins, and in the older age groups than in the youngest, where the two sexes have fins of approximately the same length. The current systematics of *artedi* has made use of the relative length of the paired fins, but has done so without reference to sex differences. If the sex ratio could be considered constant at all ages and in all populations, the errors resulting from disregard for sex differences in fin length would not be important. However, I showed in my study of the growth of the cisco that the sex ratio not only

varies widely from one population to another but also is subject to marked change within a single stock with increase in the age of the specimens. Consequently two samples from the same or from different populations may show dissimilarities that depend only on differences in the proportions of the sexes in the samples.

Other sex differences found in the cisco were limited to the Clear Lake population, in which the females possess wider and deeper bodies and slightly smaller eyes and heads than the males.

GROWTH RATE AND BODY FORM

When the four cisco populations of this investigation are arranged according to the average value of certain body ratios (marked with asterisks in Table I) they fall in the same order that they show with respect to their rates of growth. The correspondence is such that more rapid growth is associated with relatively shorter heads, maxillaries, paired fins, and dorsal fins, wider bodies, and smaller eyes (anteroposterior diameter in body length). The nature of this apparent correlation between growth rate and body form may be made clearer by examination of data on the growth rates of the four populations.

Tables III and IV present the data on the growth in length and weight respectively. It may be seen that the Clear Lake cisco has the best growth and the Trout Lake cisco the poorest with respect to both length and weight. The growth rates of the Muskellunge Lake cisco and the Silver Lake cisco are intermediate to these two extremes. Since the Muskellunge Lake cisco grows more rapidly in length than the Silver Lake cisco, though the latter has the better growth in weight, it is difficult to decide which of the two stocks does grow the more rapidly. For the purposes of this study, however, it may be considered that, if the Clear Lake cisco has the highest average value for a body ratio and the Trout Lake cisco the lowest (or the reverse), while the Silver Lake and the Muskellunge Lake populations show intermediate and similar values, then there is correlation between growth rate and that particular character.

The observed correspondence between growth rate and certain body ratios suggests the possibility that the indicated differences in body form may be, in part at least, the direct result of differences in growth rate. If such a direct relationship between growth rate and body form does exist, it may be expected that an analytic study

TABLE III

AVERAGE CALCULATED STANDARD LENGTH IN MILLIMETERS AT THE END OF EACH YEAR OF LIFE IN THE TROUT LAKE, SILVER LAKE, MUSKELLUNGE LAKE, AND CLEAR LAKE CISCO POPULATIONS

Only the Clear Lake cisco shows differences in the growth (in length) of the sexes.

Lake	Year of life												Total number of specimens
	1	2	3	4	5	6	7	8	9	10	11	12	
Trout.....	81	117	137	148	158	168	179	189	197	213	219	225	1182
Silver.....	80	129	155	169	181	189	196	...	...	...	...	...	564
Muskellunge..	96	143	161	174	...	...	...	...	...	...	...	...	1097
Clear.....	110	196	255	287	308	323	335	345	354	...	...	...	216
(male)													
Clear.....	109	199	260	291	312	326	340	351	361	369	376	...	224
(female)													

TABLE IV

WEIGHT IN GRAMS OF THE DIFFERENT AGE GROUPS OF THE TROUT LAKE, SILVER LAKE, MUSKELLUNGE LAKE, AND CLEAR LAKE CISCO POPULATIONS

Except for a tendency for the Silver Lake males to be very slightly heavier than females of corresponding age, the Clear Lake cisco is the only population to show sex differences as to growth in weight.

Lake	Age group												Total number of specimens
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	
Trout.....	...	31	37	41	47	50	...	111			119	172	933
Silver.....	..	59	68	78	93	104	...	...				...	364
Muskellunge..	..	46	51	60	...	...	...	...				...	987
Clear.....	71	267	418	578	647	673	729	796	880			...	186
(male)													
Clear.....	80	306	530	705	770	841	917	950	1085	1062	1190	...	198
(female)													

of a single population may reveal a correlation between individual growth rate and individual body form. Such analyses were conducted with respect to each ratio that showed an apparent correlation with growth rate. The details of these analyses cannot be presented in the space available here. However, the material of Table V will serve to illustrate the arrangement of data upon which the analyses were based.

TABLE V

VARIATION OF THE RATIO, L/H, IN THE CLEAR LAKE CISCO, 1937
ACCORDING TO LENGTH AND AGE

The figures in parentheses show the number of specimens.
The sexes are combined.

Length interval in millimeters	Age group									Average
	I	II	III	IV	V	VI	VII	VIII	IX	
140-59	4.53 (1)	...	...	...	...	...	...	...	...	4.53 (1)
160-79	4.54 (11)	...	...	...	...	...	...	...	...	4.54 (11)
180-99	4.46 (3)	...	...	...	...	...	...	...	...	4.46 (3)
200-19	...	4.44 (1)	...	...	...	...	...	...	...	4.44 (1)
220-39	...	4.48 (1)	...	...	...	...	...	...	...	4.48 (1)
240-59	...	4.65 (5)	4.13 (1)	...	...	...	...	...	...	4.56 (6)
260-79	...	4.70 (5)	4.39 (2)	...	...	...	...	...	...	4.61 (7)
280-99	...	...	4.57 (8)	...	3.96 (1)	...	...	...	...	4.50 (9)
300-19	...	...	4.76 (14)	4.45 (3)	4.57 (2)	4.26 (2)	4.26 (1)	...	...	4.63 (21)
320-39	...	...	...	4.58 (6)	4.59 (5)	...	4.39 (6)	4.23 (1)	...	4.50 (18)
340-59	...	...	...	...	4.49 (2)	...	4.49 (5)	4.29 (4)	4.47 (1)	4.42 (12)
360-79	...	...	...	...	...	...	4.50 (1)	4.34 (1)	4.48 (1)	4.44 (3)
380-99	...	...	...	...	...	...	4.57 (1)	...	...	4.57 (1)
Average	4.52 (15)	4.64 (12)	4.64 (25)	4.54 (9)	4.57 (10)	4.26 (2)	4.44 (14)	4.29 (6)	4.48 (2)	

This table shows the values of the ratio, head in length, for the Clear Lake cisco arranged according to length and age, that is, according to rate of growth. If the variations of L/H are examined, it may be seen, first, that in general the ratio increases with increase in length in fish of a single age group, and, secondly, that L/H decreases with increase in age in fish of a single length interval. In other words, the more rapidly growing fish within the population have the relatively smaller heads, regardless of whether the comparisons are based on fish of different lengths in the same age group or on fish of different ages in the same length group. It is true that the data exhibit certain exceptions to the general trend, but these exceptions can be explained as the result of the small number of specimens in certain groups, and can be demonstrated statistically to be of no significance. A similar relationship between relative head size and growth rate was found to exist in each of the other three cisco populations.

The studies on the relationship between growth rate and body form showed further that the more rapidly growing fish within single populations tend to possess the relatively smaller eyes and the relatively shorter maxillaries, paired fins, and dorsal fins. However, in spite of the apparent relationship between growth rate and relative body width, indicated by the averages for the entire samples of the four populations, the analysis of single populations failed to reveal any dependence of individual relative body width on individual growth rate.

Since it has been previously demonstrated by me (Hile, MS) that the growth rates of these same cisco stocks exhibit close correlation with environmental conditions, it may be concluded that environmental factors, operating through their control of growth rates, may produce extensive morphological differences between different populations of the cisco. It is probable that differences in growth rate do not account for all the differences between cisco populations of this study with respect to characters that show dependence on rapidity of growth. It must be recognized, nevertheless, that the dependence of these characters on growth rate is sufficiently marked to render them of little systematic value. The practice, common among systematic ichthyologists, of limiting comparisons to fish of approximately the same length offers no guarantee that the materials are really comparable, for fish of exactly the same size may have

widely different growth rates, and hence show pronounced but non-genetic differences in the characters that exhibit correlation with growth rate.

Five of the characters showing dependence on growth rate (relative lengths of the head, maxillary, and the paired fins, and relative size of the eye) have been employed as diagnostic characters of primary importance in the systematics of the species *artedi* (Koelz, 1931). Consequently, it must be considered probable that not a few of the *artedi* subspecies have been based on differences resulting from nongenetic differences in growth rate.

MORPHOLOGICAL DIFFERENCES BETWEEN YEAR CLASSES

In view of the apparently great sensitivity of the cisco's morphological characters to conditions of the environment, it might be expected that different year classes of the same population may exhibit, exceptionally at least, fundamental structural differences that depend on the variation from one year to another in the environmental conditions at the time of hatching and early development. Ordinarily the nature of the environment furnished by a lake does not vary greatly from year to year. However, exceptional years occur occasionally.

The data of this investigation offer one excellent example of two year classes of the same population which, though separated by only one year's difference in age, exhibit structural differences of such a fundamental nature that the individuals can be assigned readily by sight to the one group or the other. These two groups are the 1928 and 1929 year classes of the Muskellunge Lake cisco. The most striking difference between the two groups lies in the relatively much larger eye of the 1928 year class (see Pl. LXII, Fig. 3). In fresh specimens it was apparent further that the 1928 year class had a much heavier pigmentation of the dorsal region. Other differences are listed in Table VI which shows the average values, based on the 1931 collections, for each body ratio for which the two year classes exhibited statistically significant differences.

The differences indicated by the data of Table VI cannot all be considered to represent basic and permanent structural differences between the 1928 and 1929 year classes. The normal change of body proportions with growth makes it necessary to eliminate the four ratios (L/D, L/DCP, L/W, and D/E) involving measurements of

body depth and width, since the differences between the two groups with respect to these characters may be considered to depend in large measure on their differences in average length at the time of capture. The normal change of body proportions with growth does not, however, account for the differences between the two groups with respect to any of the remaining characters (L/H, L/E, H/E, H/I). It was determined further, from studies of the growth of the specimens used, that differences in the growth rates of the individuals in the samples do not account for any of the morphological differences between the 1928 and 1929 year classes.

TABLE VI

COMPARISON OF THE SAMPLES OF THE 1928 AND 1929 YEAR CLASSES (IN THE 1931 COLLECTION) OF THE MUSKELLUNGE LAKE CISCO WITH RESPECT TO THE BODY RATIOS FOR WHICH THEY SHOWED STATISTICALLY SIGNIFICANT DIFFERENCES

I = interorbital width; other abbreviations as in Table I.

Year class	Age group	Number of specimens	Body ratio								Average length in millimeters
			L/H	L/D	L/W	L/DCP	L/E	H/E	D/E	H/I	
1929	II	29	4.25	4.43	8.46	13.82	16.78	3.95	3.80	4.10	147
1928	III	81	4.17	4.82	9.20	14.27	14.95	3.58	3.12	3.94	165

Further material, collected in 1932, threw some doubt on the significance of the difference between the two year classes with respect to the relative interorbital width, but otherwise substantiated the findings based on the 1931 collection. It was concluded, therefore, that the 1928 and 1929 year classes of the Muskellunge Lake cisco show basic and permanent morphological differences with respect to eye size, head length, and heaviness of pigmentation.

The comparison of the morphometric data for the 1928 and 1929 year classes of the Muskellunge Lake cisco with corresponding data for the 1930 and 1931 year class individuals occurring in the 1932 collection from that lake indicated that the differences between the 1928 and 1929 year classes with respect to head length and eye size represent a deviation of the former group from the condition normal for the population.

A single example was observed of a probably significant difference between two year classes with respect to a numerical character. The average number of gill rakers in the 1926 year class of the Silver Lake cisco (70 specimens) was 44.53, with a probable error of ± 0.16 , while that of the 1928 year class (38 specimens) from the same lake was 45.84 ± 0.22 . There is a strong possibility that the difference of 1.31 gill rakers is significant.

The most logical explanation of the observed morphometric differences between year classes of the same population is that they had their origin in differences from one year to another in environmental conditions during the time of early development. If the environment within a single lake can vary sufficiently from year to year to produce such marked differences as those observed between the 1928 and 1929 year classes of the Muskellunge Lake cisco, it is by no means surprising to find tremendous morphological differences between cisco populations of neighboring but dissimilar lakes. There is suggested also a strong possibility that many of the morphological differences upon which the current systematics of *L. artedi* has been based represent nothing more than the direct modifying effects of different types of environments.

CONCLUSIONS CONCERNING THE SYSTEMATICS OF *LEUCICHTHYS ARTEDI* (LE SUEUR)

On the basis of the data of the present intensive morphometric study of four populations of *L. artedi* it may be concluded that the current elaborate systematization of the species set forth by Koelz (1931) is in large measure invalid. The most important reasons for this conclusion are as follows:

(1) The differences upon which the separations of many subspecies have been based are too slight and indefinite in comparison with the wide range of natural variation of the characters used. This is particularly true with respect to those subspecies that were described from the examination of very small numbers of specimens.

(2) The values of certain characters that have been used in the separation of the subspecies show a distinct dependence on growth rate.

(3) Natural changes of body proportion with increase in length and age produce greater differences between fish of different lengths in the same population than those that have been employed in the separation of some subspecies.

(4) Permanent morphological differences between different year classes of the same population may be more extensive than the recorded differences between subspecies.

(5) Separations of subspecies on the basis of the relative lengths of the pectoral and ventral fins have been made without regard for sex differences in these characters.

The contention that the current systematics of *L. artedi* is largely without validity is not intended to imply that no genetic differences exist among the various cisco forms occurring in the glacial region of North America. The long isolation of many of them in their own peculiar and special environments must have been most conducive to the origin and preservation of genetic differences among the several stocks. The detection of these genetic differences and the determination of their extent and significance, however, provide a problem of exceptional difficulty. Obviously, the assumption commonly made by systematists, that structural differences may be taken as proof of genetic differences, does not apply within the species *artedi*. The experience of continued analytic investigations may show whether the problem can be brought to any satisfactory solution. The experimental transplantation of cisco stocks to new and different environments promises to be more critically valuable. However, pending the accumulation of adequate data for the separation of *artedi* forms according to their true and natural relationships, it would appear that the designation of a local form can be made best through a description of its salient characters and a recording of the locality it inhabits.

VARIATION IN COREGONIDS

The difficulties that beset the systematic study of *Leucichthys artedi* appear to be common to the family Coregonidae, for since the time of the earliest researches on the subject the systematics of coregonids has offered the most difficult and confusing problems to its investigators. More than seventy years ago the fundamental problems of coregonid systematics were set forth clearly by Von Siebold (1863), who pointed out the confusing effects of the direct modifying action of the local environments and of the change of body proportions with age. Unfortunately, it cannot be stated that the many subsequent researches and voluminous publications have provided any sound basis for circumventing these difficulties. For

the most part the investigators of coregonid systematics have exhibited remarkable diligence in the profuse naming of species, subspecies, and varieties, but have demonstrated little enthusiasm for the laborious and time-consuming work of determining the actual degree of soundness of their classifications. Discussions of the extreme variability of coregonids have been presented repeatedly, but contributions toward the elucidation of the causes of this variability have, in general, been lacking. Morphological differences have been assumed to be infallible indexes of genetic differences, and forms have been named indiscriminately on the most tenuous grounds. The confusion created by the general penchant for "splitting" within a highly variable and plastic group has been augmented by an almost universal propensity to revise current systematics. As a result, the recognized coregonid forms are today numbered by the hundreds, and the synonymy of many of them is nothing short of appalling.

However, distinct progress toward an understanding of the true significance of coregonid variations has been made within the last quarter century. Thienemann's publication (1912) of his studies of the coregonid introduced into the Laacher See gave a first indication of the apparently great plasticity of the group with respect to the gill rakers, a character ordinarily considered very reliable for diagnostic purposes. Further evidence for a high degree of sensitivity of gill raker number and length to environmental conditions was offered by Surbeck's study (1921) of the changes that took place in *C. Schinzii helveticus* after its introduction into the Vierwaldstättersee from the Sempacher See; by Otterstrøm's comparison (1922) of brackish water and fresh-water forms of *C. lavaretus*; and by Kreitmann's observations (1929) on the changes occurring in the lavaret (*C. Wartmanni lavaretus*) on its introduction into Le Lemán from Le Bourget.

Monti's extensive studies (1929, 1930, 1933) of numerous Italian coregonid stocks, all of which originated from introductions from transalpine waters, demonstrated conclusively that, under the influence of a changed environment, coregonids may undergo extensive morphological modifications. However, these modifications are not permanent, for transplantations of the introduced forms from one Italian lake to another showed that the morphological characteristics of a single population are dependent only on the nature of the

local environment, and may be modified readily by a further change of environment.

The rapidly accumulating evidence to the effect that coregonids exhibit extensive structural modifications that represent the direct modifying effects of the environment rather than genetic dissimilarities bids fair to invalidate much of the current systematics of the group. It is quite probable that further analytic studies and transplantation experiments may show that many of the species and subspecies of coregonids recognized in Europe and America today were described on the basis of differences that are purely environmental in origin. Such artificially created groupings must inevitably fail to fulfill the primary function of taxonomy, that of setting forth phylogenetic relationships within the group. The "weeding out" of invalid species and subspecies is the most important problem confronting students of coregonid systematics today.

The simplification of the systematics of coregonids will bring about also a simplification of the problems pertaining to the evolution of the group. The previously made assumption that each of the many coregonid forms constitutes a genetically and taxonomically distinct entity has unquestionably placed unnecessarily heavy burdens on the speculative capacities of students of evolution. It is difficult to conceive how so many closely related forms could have existed as separate and distinct groups in the glacial waters of the geologically recent time of the last ice sheet. On the other hand, it is just as difficult to conceive of evolutionary development sufficiently rapid to account for the origin of the numerous present-day coregonid forms from the few basic types that might reasonably be expected to have existed in the glacial period. The most logical solution of the problem lies in the assumption that the coregonid fauna of the glacial period was represented by only a few taxonomically distinct groups, and that the number of these taxonomic groups has not increased greatly since that time. The numerous coregonid types to be observed today do not represent so many taxonomically distinct groups, but owe their existence in large measure to the fact that coregonids are subject to extensive morphological modifications which are produced by the direct action of the environment.

LITERATURE CITED

- KOELZ, WALTER N. 1931. The Coregonid Fishes of Northeastern America. Pap. Mich. Acad. Sci., Arts and Letters. 13 (1930): 303-432. Ann Arbor.
- KREITMANN, LOUIS. 1929. L'Acclimatation du lavaret du Bourget dans le Lac Lemman et sa relation avec la systématique des corégones. Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie, IV: 415-434. Roma.
- MONTI, RINA. 1929. Biologia dei coregoni nei laghi italiani. Rivista di Biologia, 11, Fasc. III-IV, V-VI, pp. 1-180. Milano.
- 1930. L'Ampiezza delle variazioni presentate dai coregoni italiani. Archivio Zoologico Italiano, 15: 83-96. Napoli.
- 1933. La genetica dei coregoni italiani e la loro variabilità in relazione coll'ambiente. Archivio Zoologico Italiano, 18, Fasc. 1-2. Napoli.
- OTTERSTRØM, C. V. 1922. Heltling (*Coregonus albula* L.) og helt (*Coregonus lavaretus* L.) i Danmark. Undersøgelser af de Ferske Vandes Fiskeriforhold, 2: 1-50. Kolding.
- SURBECK, G. 1921. Beitrag zur Kenntniss der schweizerischen Coregonen. Schweizerische Fischerei-Zeitung, 29, Nr. 3, 52-59. Bern.
- THIENEMANN, A. 1912. Die Silberfelchen des Laacher Sees. Zoologische Jahrbücher, Abt. für Systematik, 32: 173-220. Jena.
- VON SIELBOLD, CARL THEODOR ERNST. 1863. Die Süßwasserfische von Mitteleuropa. 430 pages. Leipzig.

THE INCREASE IN THE ABUNDANCE OF THE YELLOW
PIKE-PERCH, *STIZOSTEDION VITREUM* (MITCHILL),
IN LAKES HURON AND MICHIGAN, IN RELA-
TION TO THE ARTIFICIAL PROPAGATION
OF THE SPECIES

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INTRODUCTION

One of the most important problems concerning the fisheries of the Great Lakes—a problem whose solution has been too long delayed—is that pertaining to the relative effectiveness of artificial propagation and natural reproduction in the maintenance of the supply of certain commercial species. There are two important reasons for the long delay in solution of the hatchery question. First, the direct solution founded on the comparison of the percentage of fertilization of hatchery eggs and naturally spawned eggs, the relative survival of these eggs up to the time of hatching, and the relative viability of planted and wild fry is confronted with apparently insurmountable technical difficulties. Second, the indirect solution, based on the study of correlations between fry plantings and the abundance of fish in later years has been handicapped not only by the absence of reliable statistical measures of abundance but also by the lack of knowledge as to the number of years that must elapse before fry plantings can be expected to benefit the commercial stock. The technical difficulties persist, but fortunately improved methods of gathering statistics and increased knowledge of the life histories of important species have now made possible an indirect evaluation of the effectiveness of artificial propagation of some species in certain Great Lakes waters. It is the purpose of this paper to present, primarily as an illustration of method, a study of the relationship between the artificial propagation of the yellow pike-perch and recent changes in the production and abundance of this species in four fishing areas within the State of Michigan waters of Lakes Huron and Michigan.

The detailed reports of daily fishing activity that are submitted at the end of each month by every commercial fisherman licensed to fish in the Great Lakes waters under the jurisdiction of the State of Michigan make possible a rather precise estimation of annual fluctuations in the abundance of the different species in the various fishing areas, as these fluctuations are reflected in the catch per net. Both the annual records of the plantings of yellow pike-perch fry in the State of Michigan waters of Lakes Huron and Michigan, and the statistical reports employed to

follow annual fluctuations in abundance in the Michigan waters have been made available through the courtesy of the Michigan Department of Conservation.

In the treatment of the material the historical records of the production of the yellow pike-perch in Lakes Huron and Michigan will be examined first in order to establish the extent of the recent increase in the production of the species. Next, the data on changes in the abundance of yellow pike-perch, beginning in 1929, will be presented in some detail for Saginaw Bay, southern Lake Huron (Port Huron area), Green Bay and southern Lake Michigan (all waters south of Arcadia, Michigan). Finally, these recent changes in the abundance of yellow pike-perch will be examined in relation to changes in the number of fry planted in the four areas.

Although the present study is concerned primarily with fry plantings of yellow pike-perch in 1924 and later years, all available records for earlier years have been examined. Plantings of yellow pike-perch in the State of Michigan waters of Lakes Huron and Michigan prior to 1924 were so small that they could not have had much effect on the abundance of the species in these waters. The only plant made earlier than this date by the State of Michigan was a small one of 1,130,000 fry in Saginaw Bay, 1921. During the period, 1908-1919, the U. S. Bureau of Fisheries planted an average of 4,400,000 fry per year in Saginaw Bay.

PRODUCTION OF YELLOW PIKE-PERCH IN LAKES HURON (1912-1935) AND MICHIGAN, (1912-1934).

The record of the production of yellow pike-perch in the State of Michigan waters of Lakes Huron and Michigan may be found in Table 1.¹ It is at once apparent that the production of yellow pike-perch during the last several years for which data are available was well above the average in each of the two lakes.

In Lake Huron, the years, 1932-1935, represent the longest period of sustained high production of yellow pike-perch since 1912. These yields of more than a million and a half pounds are unusual, this production having been exceeded only once since 1912 when the largest recorded catch was made in 1918. Three successive large-production years occurred in 1917-1919, and yields of more than a million pounds were produced also in 1915, 1922, 1930.

In Lake Michigan, in contrast to Lake Huron, the recent increase in the abundance of yellow pike-perch in the State of Michigan waters led to an unprecedented production. The yields of both 1933 and 1934 were greater than in any preceding year of the twenty-four-year period, and the 1932 production was exceeded by that of only one year (1916).

¹ The sources of these data are as follows: The catches for Lake Huron, 1912-1933, and for Lake Michigan, 1912-1928, were taken from the reports of the Michigan Department of Conservation and its administrative predecessors. Data for the remaining years were compiled directly from fishermen's reports in the Great Lakes offices of the U. S. Bureau of Fisheries.

It should be emphasized that the increase in the production of yellow pike-perch that began in 1932 occurred simultaneously in Lakes Huron and Michigan.

The data of Table I offer a record of production only and can be taken only as roughly indicative of changes in the abundance of the yellow pike-perch. For the years prior to 1929 there are no adequate records of the fishing effort that led to the listed production. For 1929 and later years it is possible, however, to follow changes in abundance as measured by fluctuations in the catch per net. In the next section of this paper are discussed the changes in the abundance of yellow pike-perch in two fishing areas of Lake Huron during the period, 1929-1935, and two fishing areas of Lake Michigan during the period, 1929-1934.

TABLE 1. PRODUCTION IN POUNDS OF YELLOW PIKE-PERCH IN LAKES MICHIGAN AND HURON, STATE OF MICHIGAN, 1912-1935

Calendar Year	Lake Michigan	Lake Huron	Calendar Year	Lake Michigan	Lake Huron
1912	29,530	398,166	1924	46,164	503,224
1913	15,724	415,992	1925	41,637	457,628
1914	91,539	340,288	1926	58,144	815,721
1915	36,631	1,066,772	1927	24,055	901,401
1916	141,896	845,799	1928	31,832	898,955
1917	83,474	1,146,993	1929	31,088	578,187
1918	42,192	1,903,800	1930	42,303	1,115,001
1919	31,621	1,387,897	1931	50,662	846,972
1920	26,631	844,404	1932	95,475	1,571,206
1921	58,430	724,220	1933	158,960	1,656,929
1922	38,066	1,283,829	1934	156,167	1,602,856
1923	69,013	809,336	1935		1,574,031
Average				60,925	987,067

CHANGES IN THE PRODUCTION AND ABUNDANCE OF YELLOW PIKE-PERCH SINCE 1929. SAGINAW BAY

The annual production of yellow pike-perch in Saginaw Bay, the most important fishing area for the species in the State of Michigan, for the years 1929-1935, arranged according to gear is presented in Table 2. (See Fig. 1.) Well over half of the production for the seven-year period was made by shallow trap nets. The percentage of the yellow pike-perch taken in this gear increased regularly from less than thirty per cent in 1929 to almost eighty per cent in 1935. With the exception of 1931, the poundage also increased regularly. The production in the other gears varied irregularly from year to year both as to actual catch and as to the percentage of the total catch for the year. The years of lowest production were 1931 for gill nets and seines, and 1935 for pound nets. The years of highest production were 1932 for gill nets, 1929 for pound nets and 1930 for seines.

The comparison of the annual fluctuations in the production of yellow pike-perch in the different gears with the corresponding fluctuations in the catch per net (Table 3) shows that the changes of both usually proceed in the same direction.² In the seines, for example, each increase or decrease in production is accompanied by a change in the same direction in the catch per haul. The other gears, however, show exceptions to this trend. In 1933 gill nets took larger catches per net than in 1932 but had a smaller total production. The trap nets, on the other hand, took less yellow pike-perch per net in 1934 than in 1933, while at the same time the total production increased in 1934. The pound net data have exceptions in 1930 and 1934. In spite of the fact that production and the catch per unit effort commonly change in the same direction from one year to another, the production does not provide a reliable measure of abundance of fish on the grounds fished by a certain gear. As an extreme example it may be pointed out that the production of yellow pike-perch by seines in 1930 was twice that of 1934, although the catch per 100-rod haul was actually the greater in the latter year.

The difference in the average catch per unit effort in different types of fishing gear makes the direct comparison of data based on different types of gear difficult. In order to make a direct comparison possible the fluctuations in the catch per unit effort in each type of gear have been reduced to a percentage basis. The gill net data may be employed to illustrate the procedure. The average catch of yellow pike-perch per thousand linear feet of gill net over the six-year period³ 1929-1934, was 41.09 pounds. (Table 3.) The comparison of the 1929 average catch of 25.52 pounds per thousand feet of net lifted with the six-year average of 41.09 pounds shows that in 1929 the catch of yellow pike-perch per unit effort was only sixty-two per cent of the six-year average. This percentage is listed in Table 3 under the heading, "Abundance." Similarly the 1930 and 1931 catches of 40.60 and 14.05 pounds were ninety-nine and thirty-four per cent respectively of the six-year average. All the remaining percentages of abundance recorded in the table for the different gears were obtained by the same method.

The detailed discussion of the abundance (percentages) should be preceded by some consideration of the relative degree of reliability of the data based on different types of gear. Of the four gears the shallow trap probably offers the most reliable information, because it produced more than half of the yield of yellow pike-perch and because this species is one of the most important in its catch. The gill net data offer a reliable measure of the relative abundance of yellow pike-perch in the April spawning run. Practically all yellow pike-perch produced by this gear are taken in April, and the recorded catches per unit effort are

² The catches per unit effort in Tables 3, 5, 7 and 8 are the number of pounds of yellow pike-perch per 1,000 linear feet of gill net lifted, per single net lift of impounding nets (shallow traps, pounds, fykes), and per haul of a 100 rod seine.

³ The six-year period was employed because the 1935 data are not yet available for Lake Michigan.

accordingly based on the gill net fishery of this single month. The data from the seine are much less reliable than those from gill nets and trap nets, first, because the seine accounts for only a small part of the total yellow pike-perch production, and, second, because the catch of yellow pike-perch constitutes a relatively unimportant part of the total production of seines.

The pound net data, because of their disagreement with those of other gears, require special consideration. In spite of the fact that pound nets took a fifth of the yellow pike-perch produced in the seven-year period, there is some reason to question the reliability of the estimates of fluctuations in abundance based on this gear. Following the introduction of the deep-water trap net into the region of Lake Huron off Saginaw Bay in 1930 (because of legal restrictions very few deep trap nets were fished in the bay proper) there occurred a pronounced decline in the number of large-mesh pound nets fished. This decline, which entailed the withdrawal from operation of the pound nets that were most effective in the capture of yellow pike-perch, was proceeding most rapidly at the time of the most rapid increase in the abundance of this species. It is believed that this removal of the most effective nets from the pound-net fishery accounts for the discrepancies between the pound net data and those of other gears. Consequently, no high degree of dependence can be placed on the data of abundance computed from the catch of pound nets. However, in the absence of definite proof of the unreliable nature of the pound-net data, they have been included in the computation of average abundance.

The computation of the average abundance for a single year consists of balancing the total catch of the gears included in the analysis against the catch they would have been expected to take had abundance been exactly at the six year average. For example, the computation of the average abundance for 1929 is made as follows:

$$\frac{(116,768 + 180,131 + 293,523 + 31,067) \times 100}{\frac{116,768}{25.52} \times 41.09 + \frac{180,131}{14.56} \times 34.54 + \frac{293,523}{17.86} \times 21.12 + \frac{31,067}{24.91} \times 52.82} = 60.4.$$

The corresponding computations for the next five years yielded the following percentages:

1930— 87.5	1933—144.8
1931— 55.5	1934—136.5
1932—125.0	

The sum of the six percentages is 609.7. In order that their mean may be 100, each is multiplied by the factor,⁴ $\frac{600}{609.7} = 0.984$.

⁴ In numerous computations of this type the "factor" has been found to be so closely about the value, 1,000, that its use probably represents an unnecessary refinement. The correction represents merely an adjustment within the period selected for the establishment of "average" conditions.

With the discussion of the preceding paragraphs kept in mind, it is now possible to estimate the changes in the abundance of the yellow pike-perch in Saginaw Bay over the seven year period, 1929-1935. (Table 3 and Fig. 1.) It should be kept in mind that all percentages have been computed with reference to the six-year average (1929-1934). The 1929 abundance of yellow pike-perch was relatively low (fifty-nine); shallow traps and seines were particularly unsuccessful. In 1930 the catch of all gears except pound nets showed marked improvement, and the general abundance (eighty-six), computed from all gears, rose to within fourteen per cent of average. The catches of all gears fell off so sharply in 1931 that the average abundance (fifty-five) fell below even that of 1929. All gears were so much more successful in 1932 than in 1931, that the general or average abundance rose from fifty-five to 123. This increase continued, although to a lesser degree, in 1933. Three of the gears registered declines in abundance in 1934 and the general abundance fell from 143 to 134. The general abundance dropped again in 1935, but this decrease can be traced entirely to the very poor catches of pound nets. Since, as has been pointed out, there is some question concerning the reliability of the pound-net data, and since the catches of the other three gears all showed improvement, it may be concluded that the abundance of yellow pike-perch in Saginaw Bay was greater in 1935 than in 1934. It is not likely, however, that the 1935 abundance was as great as that of 1933.

A very interesting feature of the data is the close correspondence between changes in total production (Table 2) and general abundance (Table 3). This agreement suggests the possibility that, in some fisheries, production statistics alone may serve as a fairly reliable index of fluctuations in abundance.

TABLE 2. PRODUCTION OF YELLOW PIKE-PERCH IN SAGINAW BAY, 1929-1935

Calendar Year	Production in Pounds by Gear					Total Production
	Large Mesh Gill Net	Shallow Trap	Pound	Seine	All Others	
1929	116,768	180,131	293,523	31,067	10,262	631,751
1930	131,337	434,408	284,102	149,803	4,153	1,003,803
1931	36,051	330,621	183,071	25,098	106,529	681,370
1932	167,945	799,989	224,966	45,113	136,534	1,374,547
1933	108,126	848,248	278,794	91,571	128,033	1,454,772
1934	92,988	951,021	201,233	74,542	29,570	1,349,354
1935	101,393	1,016,324	84,263	75,150	15,549	1,292,679
Percentage	9.7	58.5	19.9	6.3	5.6	100.0

TABLE 3. AVERAGE ANNUAL CATCH PER LIFT OR PER SEINE HAUL OF YELLOW PIKE-PERCH IN SAGINAW BAY, 1929-1935, AND ANNUAL FLUCTUATIONS IN THE ABUNDANCE OF FISH ON THE GROUNDS

Calendar Year	Average Catch per Net or per Seine Haul, in Pounds				Abundance				
	Large Mesh Gill Net	Shallow Trap	Pound	Seine	Large Mesh Gill Net	Shallow Trap	Pound	Seine	Average (General)
1929	25.52	14.56	17.86	24.91	62	42	85	47	59
1930	40.60	26.20	18.23	73.68	99	76	86	139	86
1931	14.05	20.90	12.82	16.14	34	61	61	31	55
1932	57.22	45.84	22.44	43.24	139	133	106	82	123
1933	59.22	52.27	26.72	80.39	144	151	126	152	143
1934	49.94	47.46	28.62	78.58	122	137	136	149	134
1935	53.64	49.18	12.36	86.06	131	142	59	163	130
Average for 1929-1934	41.09	34.54	21.12	52.82	100	100	100	100	100

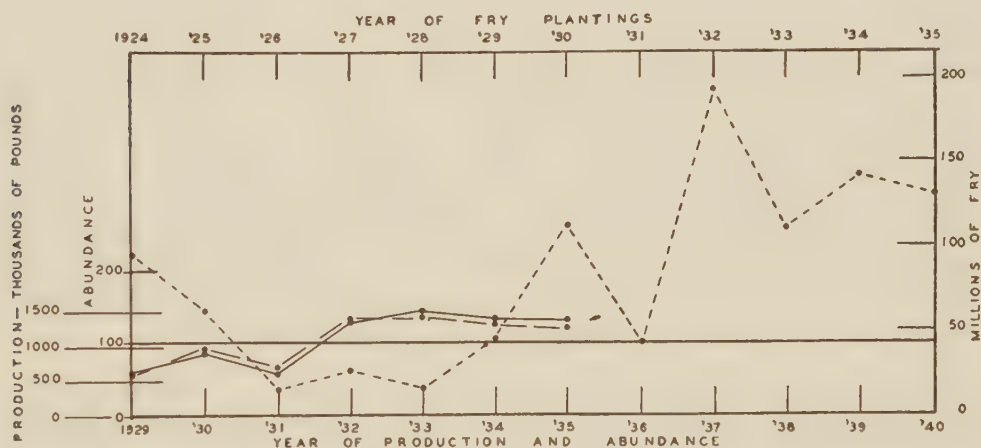


Fig. 1. Production—and abundance—of yellow pike-perch in Saginaw Bay, 1929-1935.

The comparison of the data by periods reveals that in the four years, 1932-1935, the abundance of yellow pike-perch in Saginaw Bay was approximately twice that of the three-year period, 1929-1931. It is this increase that has been so generally considered the result of fry plantings in the area.

SOUTHERN LAKE HURON

This area includes all State of Michigan waters of Lake Huron south of Forester, Michigan. Eighty per cent of the yellow pike-perch produced in the seven years, 1929-1935, was taken in shallow trap nets and fyke nets (Table 4). Unfortunately, however, the shallow trap-net data

TABLE 4. PRODUCTION OF YELLOW PIKE-PERCH IN SOUTHERN LAKE HURON, 1929-1935

Calendar Year	Production in Pounds by Gear			Total Production
	Shallow Trap	Fyke	All Others	
1929	341	23,384	10,320	34,045
1930	1,650	35,818	6,911	44,379
1931	1,399	53,085	10,793	65,277
1932	5,349	54,535	17,202	77,086
1933	42,063	54,672	11,355	108,090
1934	72,911	42,351	47,354	162,616
1935	132,274	31,252	34,820	198,346
Percentage	37.1	42.8	20.1	100.0

can not well be employed for the estimation of changes in abundance. For all practical purposes the shallow trap-net fishery of the region may be considered to have started in 1933.⁵ In this year 31,965 pounds of the listed catch of 42,063 pounds were taken by a single operator in a single month. This phenomenal success in fishing the spawning run (the average lift per net was 266 pounds) accounts for the large value of the average lift of trap nets in 1933 (Table 5). Had this one fisherman not operated during this single month the average lift of yellow pike-perch in shallow trap nets for 1933 would have been eleven pounds. In 1934 and 1935 shallow traps were fished more extensively, by more operators, and over a longer season than in 1933. Consequently, in spite of the continued expansion of the fishery in 1935, the 1934 and 1935 data for the shallow trap can probably be compared.

TABLE 5. AVERAGE ANNUAL CATCH PER LIFT OF YELLOW PIKE-PERCH IN SOUTHERN LAKE HURON, 1929-1935, AND ANNUAL FLUCTUATIONS IN THE ABUNDANCE OF FISH ON THE GROUNDS

Calendar Year	Average Catch per Net in Pounds		Abundance	
	Shallow Trap	Fyke	Shallow Trap	Fyke
1929	2.66	20.80	8	73
1930	10.18	17.91	29	63
1931	12.38	25.62	36	90
1932	20.33	25.78	58	90
1933	122.43	33.38	352	117
1934	40.82	47.85	117	167
1935	58.97	38.49	169	135
Average for 1929-1934	34.80	28.56	100	100

⁵ The shallow traps fished in earlier years were largely "gobblers," or small nets with pots usually 4 to 6 feet deep. These nets have a fishing power approximately equal to that of a fyke net, and can not be compared with the true shallow trap.

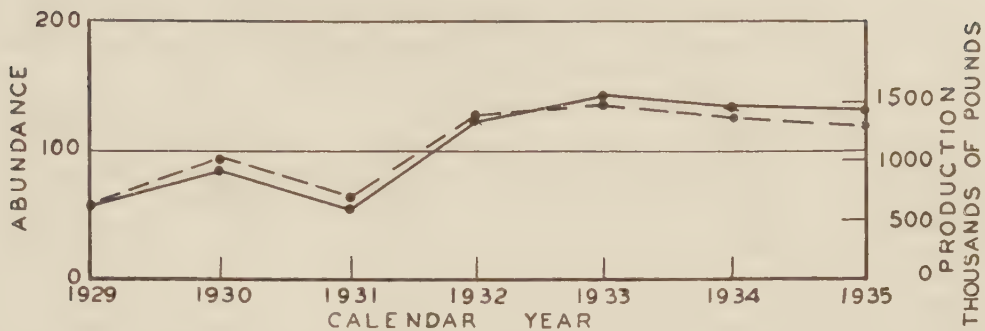


Fig. 2. Production—and abundance (fykes—, shallow traps . . .) of yellow pike-perch in southern Lake Huron, 1929-1935.

According to the fyke-net data the abundance of yellow pike-perch in southern Lake Huron decreased slightly from 1929 to 1930, rose to within ten per cent of the 1929-1934 average in 1931 and remained at this level in 1932, increased rather sharply in 1933 and 1934, and fell off considerably in 1935 (Table 5, Fig. 2). The shallow trap-net data for 1934 and 1935 throw some doubt on the 1935 decline indicated by the fyke-net data. The data as a whole show that there has been a sharp increase in the abundance as well as in the production of yellow pike-perch in southern Lake Huron. This increase resembles closely that observed in Saginaw Bay, although it appears to have occurred a year later in 1933. The production and abundance curves for southern Lake Huron do not show very close agreement.

GREEN BAY

Data on the production of yellow pike-perch in the State of Michigan waters of Green Bay are presented in Table 6 (Fig. 3). Although the production of this area is not large, it is noteworthy that the relative increase in production was more pronounced here than it was for the corresponding period in Saginaw Bay and southern Lake Huron. In Green Bay the catch of yellow pike-perch in the three year period, 1932-1934, was more than three times that of the years, 1929-1931. The most important gear for the production of yellow pike-perch in the area was the fyke net, followed in order by the pound net and the shallow trap net.

The computations of annual fluctuations in abundance have been based on the catch per unit effort of the three types of nets just mentioned (Table 7, Fig 3). The abundance percentages for the two leading gears, pounds and fykes, agree rather well, but the data for both of these types of net disagree with those of the shallow trap. This disagreement is particularly prominent for the 1931 and 1934 data. No plausible explanation of the discrepancies presents itself. It should be remembered, however, that the shallow trap net produced only a small part of the

TABLE 6. PRODUCTION OF YELLOW PIKE-PERCH IN GREEN BAY, MICHIGAN, 1929-1934

Calendar Year	Production in pounds by gear				Total Annual Catch
	Shallow Trap	Pound	Fyke	All Other	
1929	7,244	7,171	6,557	5,991	26,963
1930	5,036	6,294	12,646	3,470	27,446
1931	5,379	13,876	19,543	2,671	41,469
1932	7,929	29,586	44,768	2,776	85,059
1933	17,538	36,687	52,546	1,339	108,110
1934	17,239	25,916	61,182	3,910	108,247
Percentage	15.2	30.11	49.6	5.1	100.0

TABLE 7. AVERAGE ANNUAL CATCH PER LIFT OF YELLOW PIKE-PERCH IN GREEN BAY, MICHIGAN, 1929-1934 AND ANNUAL FLUCTUATIONS IN THE ABUNDANCE OF FISH ON THE GROUNDS

Calendar Year	Average catch per net in Pounds			Abundance			Average (General)
	Shallow Trap	Pound	Fyke	Shallow Trap	Pound	Fyke	
1929	3.71	10.80	15.43	40	57	43	47
1930	4.55	7.39	20.17	49	39	56	50
1931	10.21	10.96	27.27	109	58	76	73
1932	9.85	19.60	37.00	105	103	103	106
1933	19.20	33.27	56.56	205	175	157	174
1934	8.61	31.76	59.34	92	168	165	150
Average	9.36	18.96	35.96	100	100	100	100

total yellow pike-perch catch. It is also true that this species constitutes a relatively unimportant part of the total catch of shallow traps. Consequently, the shallow trap-net data may be considered less reliable than data based on pound-net and especially fyke-net catches. The small catches of yellow pike-perch in trap nets in 1934 account in large measure for the drop in the general abundance of the species in that year.

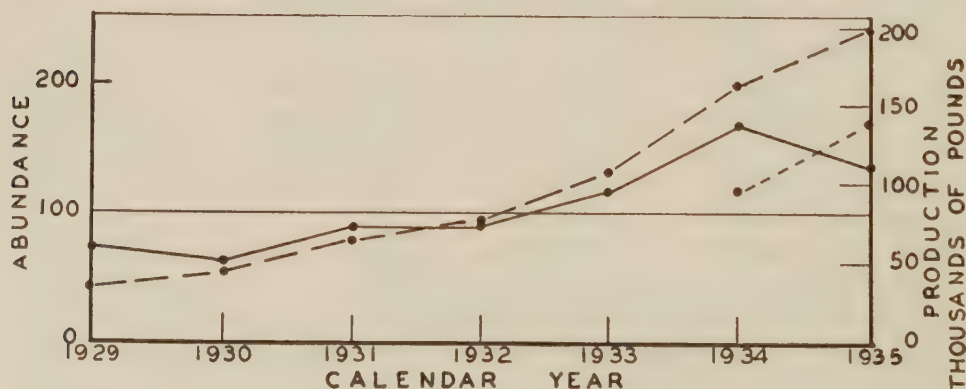


Fig. 3. Production—and abundance—of yellow pike-perch in Green Bay, 1929-1934.

The comparison of the changes in the abundance of yellow pike-perch in Green Bay with those of Saginaw Bay over the same period of time brings out a close resemblance between the two sets of data. A recent pronounced increase in abundance occurred simultaneously in these two widely separated areas. This increase in abundance was relatively the greater in Green Bay. The Green Bay data resemble the Saginaw Bay data in showing a close agreement between fluctuations in production and general abundance.

SOUTHERN LAKE MICHIGAN

This area includes all State of Michigan waters of Lake Michigan south of Arcadia, Michigan (ten miles south of Frankfort). Data on both production and abundance of yellow pike-perch in the region for the years, 1929-1934, may be found in Table 8. (Fig. 4). The total production of yellow pike-perch in this region was small throughout the six-year period, but the relative increase in production in the more recent years was very large. The catch of yellow pike-perch in the three years, 1932-1934, was more than four and one-half times that of 1929-1931. In spite of the inclusion of the poor year, 1932, this is the largest relative increase in production found in any of the four areas considered.

The pound net was the only type of gear that took yellow pike-perch in sufficient quantities to serve as a basis for the estimation of annual fluctuations in abundance, and even in this gear the production was so small that the data must be recognized as indicative of trends rather than descriptive of detail. The data for 1929 were included only for the sake of completeness. In spite of the criticisms to which the abundance data are subject, they serve to show conclusively that the large increase in the production of yellow pike-perch in 1933 and 1934 was accompanied by a large increase in the abundance of the species.

It should be noted that southern Lake Michigan and southern Lake Huron agree in showing a pronounced upturn in the abundance of yellow pike-perch in 1933, a year later than in Saginaw Bay and Green Bay.

TABLE 8. PRODUCTION AND CHANGES OF ABUNDANCE OF YELLOW PIKE-PERCH IN SOUTHERN LAKE MICHIGAN, 1929-1934

Calendar Year	Production in Pounds by Gear			Average Catch in Pounds	Abundance
	Pound	All Others	Total	Pound Nets	Pound Nets
1929	866	1,132	1,998	11.55	71
1930	10,616	2,918	13,534	12.79	79
1931	5,252	1,314	6,566	7.20	45
1932	7,925	1,638	9,563	9.00	56
1933	41,565	4,686	46,251	27.71	171
1934	33,210	12,464	45,674	28.85	178
Percentage	80.5	19.5	100.0	16.18*	100*

* Average

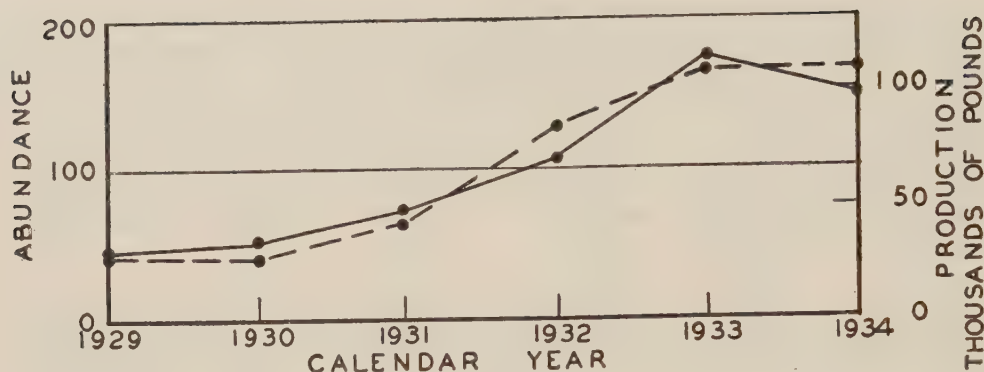


Fig. 4. Production—and abundance—of yellow pike-perch in southern Lake Michigan, 1929-1934.

FRY PLANTING AND CHANGES IN ABUNDANCE

In the preceding pages it was established definitely that the recent increase in the production and abundance of the yellow pike-perch was by no means confined to Saginaw Bay, the chief production center for the species in the State of Michigan waters of the Great Lakes. Equally pronounced relative increases in both production and abundance occurred simultaneously in southern Lake Huron, Green Bay, and southern Lake Michigan. This situation has been generally overlooked since the production and abundance of yellow pike-perch in regions other than Saginaw Bay were always so small that even a large *relative* increase in abundance did not raise this species to a position of importance in the fishery. The fact that the increase in abundance was general rather than local suggests strongly that the causes operative in the different areas may have been the same.

There exists a rather general belief, particularly among commercial fishermen, that the increase in the abundance of yellow pike-perch in Saginaw Bay is the direct result of the artificial propagation of the species. It is probable, however, that this belief is based largely on the concomitant increase in production and artificial propagation, without due regard for the necessary period of time that must elapse before fry plantings can be expected to affect the commercial stock. For example, an article entitled, "Pickerel Propagation in Saginaw Bay," (*Great Lakes Fisherman*, June, 1936) contains the following statement: "..... it is significant for the fishermen to note that the amount of fish produced is directly proportional to the number of spawn planted each preceding year." This statement carries the obviously absurd implication that the yellow pike-perch of Saginaw Bay attains the legal size of one and one-half pounds within a single year. Certainly, any correlation between fry plantings and the commercial catch must include consideration of the time actually necessary for fry to grow to fish of legal size.

It is the purpose of this section to examine the recent changes in the abundance of yellow pike-perch in relation to the extent of the fry plantings that may reasonably be expected to have contributed to the changes. From records of age determinations on Saginaw Bay pike-perch on file in the Great Lakes offices of the Bureau of Fisheries it was determined that legal size is attained in approximately five years (in the sixth year of life). The age at which the yellow pike-perch attains legal size in other localities of Lake Huron and Michigan probably does not vary more than a year from that of the Saginaw Bay fish.⁶ Although the effects of fry planting may be expected to show up first after a lapse of five years, these effects might carry over for one or two or even more additional years.

SAGINAW BAY

Data for the examination of the relationship between fry plantings and the abundance and production of yellow pike-perch in Saginaw Bay are presented in Table 9 and shown graphically in Fig. 5. The arrangement is such that each fry planting may be compared directly with the abundance and production five years later.

The examination of Table 9 and Fig. 5 reveals little to support the belief that the recent increase in the abundance of yellow pike-perch has resulted from artificial propagation. The fry plantings dropped from ninety-four million in 1924 to sixty-one million in 1925, but the abundance of yellow pike-perch increased from fifty-nine in 1929 to eighty-six in 1930. This increase might well be explained, however, as the result of two successive large plants (1924 and 1925). It would appear, however, that the effects of neither the 1924 nor 1925 catch extended to the 1931 season, for with the reduction of the plant to fifteen million fry in 1926 the abundance of fish in 1931 dropped to the low value of fifty-five. The fry plants continued to be small in both 1927 and 1928, but nevertheless, the abundance of yellow pike-perch increased tremendously in 1932 and 1933. The numbers of fry planted were increased in 1929 and 1930, but the abundance of yellow pike-perch declined slightly in 1934 and possibly in 1935. (See p. 14). These correlations, far from supporting the belief that artificial propagation increases the abundance of the stock, tend to show an inverse relationship between the numbers of fry planted and the abundance of fish in later years. If this extreme interpretation is not acceptable, it must be admitted, at least, that the evidence does not point toward any beneficial effects of fry planting.

It may be argued, of course, that the maximum effect of fry plantings appears a year or so later than the year in which the fish reach legal size. This argument has no effect on the conclusions of the preceding

⁶ The belief that the growth of the yellow pike-perch does not vary widely in different Great Lakes areas is supported by the fact that the yellow pike-perch of Lake Erie attains a weight of twenty-four ounces in about five years. (Deason, H. J., MS., *Morphometric and Life History Studies of the Pike-Perches (Stizostedion) of Lake Erie*.)

paragraph, for the rearrangement of the data of Table 9 with six or seven years as the interval would not change the conclusion that high abundance was correlated with small fry plants.

Unquestionably it would be most desirable to have data of the type presented in Table 9 and Fig. 5 covering a period of more than six years. With the passage of time this extension of the data will be possible and the blank spaces of the table and figure will be filled. If artificial propagation has any important effect on the abundance, it may be expected that the large fry plantings of 1931-1935 will lead to a sustained high abundance of yellow pike-perch through the period, 1936-1940. Should the abundance decline to a low level within this period the inescapable conclusion will be that fry plantings have no significant effect on the abundance of the commercial stock.

TABLE 9. RELATIONSHIP BETWEEN FRY PLANTINGS AND THE ABUNDANCE AND PRODUCTION OF YELLOW PIKE-PERCH IN SAGINAW BAY

Fry Plantings		Abundance and Production		
Year	Number*	Abundance	Production†	Year
1924	94	59	632	1929
1925	61	86	1,004	1930
1926	15	55	681	1931
1927	26	123	1,375	1932
1928	15	143	1,455	1933
1929	45	134	1,349	1934
1930	112	130	1,293	1935
1931	43			
1932	191			
1933	110			
1934	140			
1935	130			

* Millions of fry

† Thousands of pounds

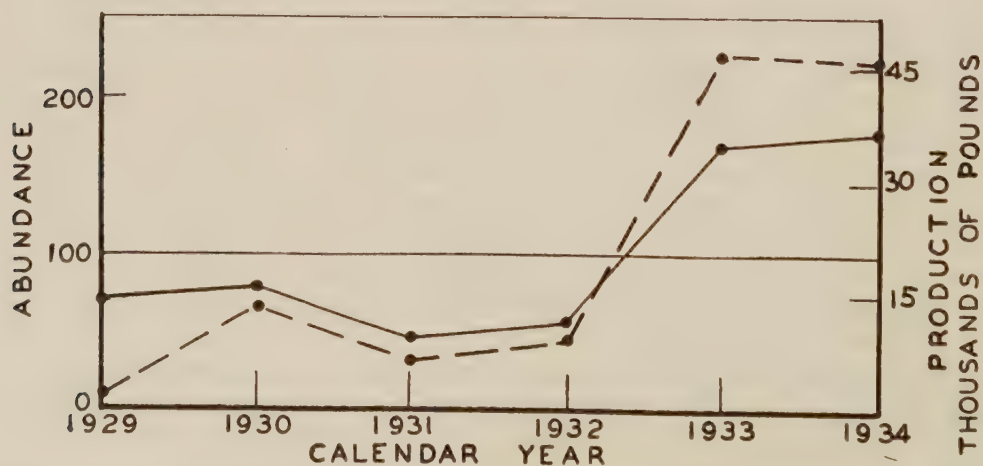


Fig. 5. Relationship of fry plantings—, abundance—, and production— of yellow pike-perch in Saginaw Bay.

SOUTHERN LAKE HURON

Since there are no records of pike-perch plantings in southern Lake Huron, the recent increase in the abundance of yellow pike-perch in this region (Table 5) represents nothing more than a natural fluctuation in abundance. Any contention that the waters received benefits from Saginaw Bay plantings by means of migration loses force by reason of the strong evidence that Saginaw Bay, itself, did not benefit from these plantings.

GREEN BAY

The only record of a yellow pike-perch plant in the Michigan waters of Green Bay is that of 1,500,000 fry planted in 1930. Even if it is assumed that this single small plant might affect the abundance of the yellow pike-perch in the region, it must be recognized that the introduction occurred too late to play any part in the recent increase in the abundance of the species. The increase, then, must be considered to represent only a natural fluctuation. It is of particular importance to note that the increase in abundance in Green Bay, which is wholly traceable to natural causes, is relatively more pronounced than the increase that occurred in Saginaw Bay, the center of artificial propagation activities.

SOUTHERN LAKE MICHIGAN

Although there are no records of yellow pike-perch plantings in the waters of southern Lake Michigan numerous plants have been made in tributary rivers and in inland lakes with direct communication with Lake Michigan. The probability that the fry from these relatively small plantings found their way into Lake Michigan in sufficient numbers to account for the recent increase in the abundance of yellow pike-perch in the region is remote. Nevertheless, in the interest of a thorough analysis, a comparison of these plantings with the changes in abundance in southern Lake Michigan is presented in Table 10. The data of this table do not indicate that fry plantings in tributary waters had any effect on the abundance of the yellow pike-perch in southern Lake Michigan. On the contrary, the high abundance of 1933 and 1934 occurred at a period when a decline in abundance would be expected.

The argument for the effectiveness of artificial propagation might be improved by extending the assumed period of time necessary for the fish to reach commercial size to six or seven years. Even this improved argument does not stand up well before the opposing arguments that the fry plantings were very small, and that they were not actually made in Lake Michigan. Another argument against the explanation of the 1933-1934 abundance as the result of fry plantings lies in the fact that the 1925-1927 plantings were no larger than those

made in most of the earlier years, but often were smaller. For example, the average numbers of fry planted per year by the State of Michigan in waters tributary to southern Lake Michigan by 6-year periods were: 1918-1923, 527,000 fry; 1912-1917, 502,000 fry; 1906-1911, 977,000 fry. These earlier plantings were probably not very effective, for an examination of Table 1 shows that in many of these earlier years the production of all Lake Michigan, including Green Bay, was less than the production of southern Lake Michigan alone in 1933 or 1934. The logical conclusion, therefore, appears to be that in southern Lake Michigan as in Saginaw Bay, southern Lake Huron, and Green Bay the recent increase in the abundance of the yellow pike-perch represented only a natural fluctuation.

This agreement of the results for all four areas leads to the conclusion that the recent general increase in the abundance and the production of yellow pike-perch in the State of Michigan waters of Lakes Huron and Michigan represented a natural fluctuation in abundance, and did not have its origin in the artificial propagation of the species.

TABLE 10. RELATIONSHIP BETWEEN THE ABUNDANCE AND PRODUCTION OF PIKE-PERCH IN SOUTHERN LAKE MICHIGAN AND THE PLANTINGS OF FRY IN TRIBUTARY WATERS

Fry Plantings		Abundance and Production		
Year	Number*	Abundance	Production†	Year
1924		71	2	1929
1925	375	79	14	1930
1926	320	45	7	1931
1927	950	56	10	1932
1928		171	46	1933
1929		178	46	1934
1930				
1931	722			
1932	2,340			
1933	4,900			
1934	2,885			

* Thousands of fry

† Thousands of pounds

SUMMARY

1. Attention is called to the importance of the problem concerning the effectiveness of artificial propagation and fry planting for the maintenance of the stock of commercial species of fish in the Great Lakes waters.

2. A method is proposed for the solution of the problem by means of a comparison of the known quantities of fry planted in different years with fluctuations in the abundance of fish in later years. The fluctuations in abundance are determined from the analysis of commercial fisheries statistics.

3. The specific application of the method to the yellow pike-perch

leads to the conclusion that the recent general increase in the abundance of this species in the State of Michigan waters of Lakes Huron and Michigan was not the result of artificial propagation, but, rather, represented a natural fluctuation in abundance.

DISCUSSION

MR. LESTER SMITH (Wisconsin): The fishing for yellow pike has been in the region of Saginaw Bay. I was told that the large percentage of this spawn was sent to inland waters of the lakes. Are you taking that into consideration?

DR. HILE: In earlier years, yes, practically all, but to-day the percentage to inland lakes would be negligible in proportion to the total amount of production. The plantings in recent years have been running in the neighborhood of a couple of hundred million fry; I think you will find that the inland lakes do not get any quantity approaching that at all.

MR. LESTER SMITH: Wisconsin only, up to the last year, has required compulsory reports on the part of the fishermen. What sources of information did you go to for your statistics on Green Bay and lower Lake Michigan?

DR. HILE: I intended to make that clear. Southern Lake Michigan, the west part of the lake south of Arcadia, is the region I took, down to the Indiana line.

MR. LESTER SMITH: Green Bay waters are largely in Wisconsin.

DR. HILE: Wisconsin does not produce pike perch.

MR. LESTER SMITH: Not very many.

DR. BELDING: Has Dr. Hile figures back far enough to determine whether there is an any cyclic trend in quantities of fish in the lake? These figures are rather striking, as they run practically parallel to the cyclic trends in the Atlantic salmon.

DR. HILE: In trying to work out cycles in the Great Lakes we are handicapped by having nothing more than production statistics, and production statistics are in no sense a certain measure of the abundance of fish. Certain cycles have occurred but there are economic factors that we know have intervened. For example, in western Lake Erie there was a large production of fish during the bitterest years of the depression, but the abundance underwent practically no change, which simply meant that a lot of people were in a bad way financially and were doing no fishing. As industrial conditions in that region improved, production went down. I think it is a very delicate proposition to try to measure abundance merely through production.

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Morphometry of the cisco, *Leucichthys artedi* (Le Sueur), in the lakes of the Northeastern Highlands, Wisconsin.¹⁾

By

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With 61 tables on 3 plates and 5 figures.

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Introduction.

In an earlier study (Hile, 1936) a detailed investigation was presented of the age and growth of the ciscoes of Trout Lake, Muskellunge Lake, Silver Lake, and Clear Lake in northeastern Wisconsin. It was demonstrated that the growth rate of the cisco varies widely from lake to lake within the same geographical area, and that these differences in growth rate show a close correlation with

¹⁾ Published by permission of the U. S. Commissioner of Fisheries.

certain environmental conditions. The present study of the morphometry of the cisco populations of these same four lakes may be considered a continuation of the earlier investigation, since emphasis will be placed on the problem of the relationship between the growth rate and morphological characteristics of the cisco. Attention will be given also to the existence of fundamental structural differences between year classes of the same population, differences that must be considered the result of variation from one calendar year to another in the environmental conditions at the time of the early growth and development of the cisco.

The lakes whose cisco populations were investigated were not chosen at random but were selected as „type“ lakes. Trout Lake is the second largest and the deepest lake in the highland district. Its waters have, for the lakes of

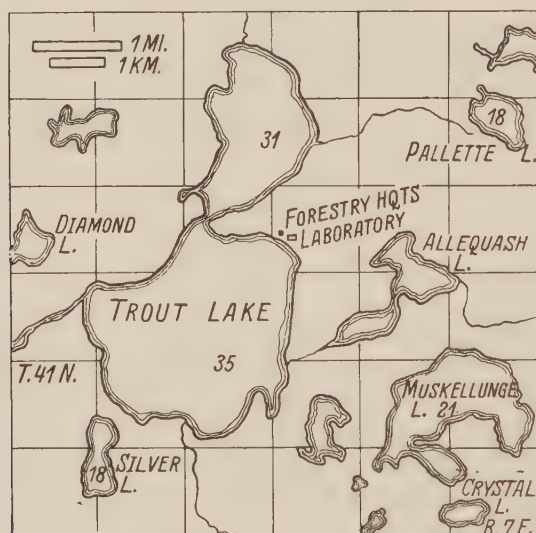


Figure 1. — Map of Trout Lake and vicinity. The maximum depths in meters are indicated for Palette Lake, Muskellunge Lake, Silver Lake, and both basins of Trout Lake.

this region, a relatively high concentration of bound CO_2 . Muskellunge Lake is intermediate with respect both to size and the hardness of its waters. Silver Lake is also intermediate as to the concentration of bound CO_2 in its waters, but is quite small in size. Clear Lake has exceptionally soft water, and is the largest lake of this type in the highland district.

All four lakes lie within short distance of each other. Trout Lake (See Figure 1), the location of the limnological laboratories of the Wisconsin Geological and Natural History Survey, is situated near the center of Vilas County in the heart of the northeastern highlands lake district. Silver Lake lies about one kilometer off the southwest corner of Trout Lake; Muskellunge Lake lies about three kilometers due east of the south basin of Trout Lake; and Clear Lake (See Figure 2) is located about thirteen kilometers southeast of Trout Lake.

Table 1 gives further data concerning these four lakes. These data were supplied by Dr. Chancey Juday from the records of the Wisconsin Geological and Natural History Survey. The values for pH, conductivity, color, bound CO₂, and organic matter of the plankton refer to average surface conditions. The pertinent data with respect to Trout Lake are those concerning the south basin, in which portion of the lake all cisco samples were taken.

Koelz (1931), in his study of the coregonids of northeastern America, examined collections from each of the four lakes. It is in this publication that Koelz described the subspecies *clarensis* for which Clear Lake is the type locality. Koelz also assigned the Muskellunge Lake and the Silver Lake ciscoes to the subspecies *clarensis*. He considered the Trout Lake cisco a member of the subspecies *clemensi*, which he also described in his 1931 publication.

Because of the differences in the classification of coregonids in Europe and America, attention should be given to the position of the cisco or lake herring, *Leucichthys artedi*, within the family Coregonidae. The genus *Coregonus* as recog-

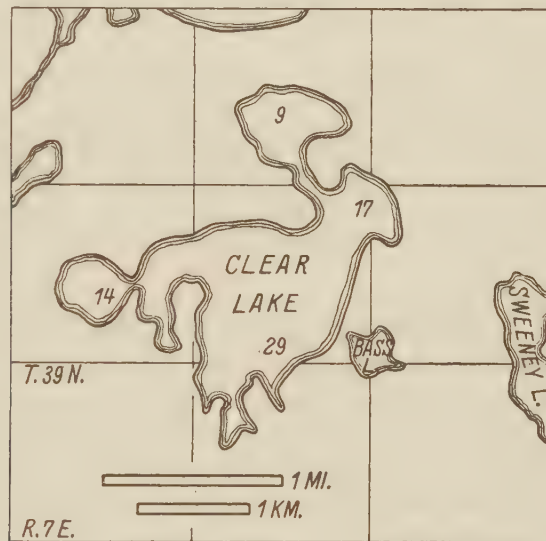


Figure 2. — Map of Clear Lake and vicinity. The maximum depths in meters are indicated for the various areas of Clear Lake.

nized by European ichthyologists includes the American genera, *Coregonus* and *Leucichthys*. The American genus *Coregonus* would fall under the European sub-genus *Coregonus*, while *Leucichthys* would fall under the sub-genus *Argyrosomus*, of the European ichthyologists. (Because of preoccupation the name *Argyrosomus* is not employed by American ichthyologists in the systematics of the Coregonidae.) The nearest European relatives of the American lake herring or cisco (*Leucichthys artedi*) appear to be the European lake herring or „kleine Maräne“ (*Coregonus albula*), the vendace (*Coregonus vandesius*), and the pollan (*Coregonus pollan*).

Acknowledgements.

I wish to acknowledge the assistance and co-operation of the members of the staff of the Wisconsin Geological and Natural History Survey²⁾. Dr. Chancey Juday gave valuable assistance in the selection of „type“ lakes for study and made available important limnological data from the records of the Survey. Dr. Edward Schneberger made all the 1932 collections of preserved specimens.

Dr. Carl L. Hubbs, Curator of Fishes in the Museum of Zoology at the University of Michigan, gave valuable advice both as to the methods of making measurements and counts and as to methods of analysis of the morphometric data, and made helpful criticisms of the original manuscript.

Dr. John Van Oosten, in charge of the Great Lakes investigations of the Bureau of Fisheries, examined the original manuscript critically and made valuable suggestions for its improvement.

Dr. Peter Okkelberg, secretary of the Graduate School of the University of Michigan, verified the accuracy of my translation of parts of Otterstrøm's (1922) publication. The reference to Olofsson's (1932) paper is based on an abstract prepared by Mr. R. W. Eschmeyer of the Michigan Institute for Fisheries Research.

I wish to acknowledge particularly the assistance of Mr. William Duden, formerly research assistant in the Bureau of Fisheries, who made all the measurements and counts upon which this morphometric study is based. Not only did Mr. Duden's careful and accurate work guarantee a high degree of dependability for the original data of the investigation, but his observations and suggestions were of great value in the analysis of these data.

Variation in the Coregonids.

Since the times of the earliest studies of the subject, the systematics of the coregonids has offered the most difficult and confusing problems to its investigators. Although the extensive researches of the last several decades have added greatly to the amount of data available with respect to this troublesome group, the problem of the true taxonomic relationships of the many coregonid forms still awaits its proper solution.

Present-day investigators of the coregonids agree rather generally that the systematics of the group is in a highly unsatisfactory state of confusion, and further that the clarification of this confusion presents problems more or less unique in the field of taxonomy. It has been observed repeatedly that coregonids can not be subdivided readily into species and subspecies in the ordinary sense of the word. Typical of the opinion of modern workers on this point is Thiene-mann's (1928) observation: „Der ‚Artbegriff‘ im landläufigen Sinne ist innerhalb der Gattung *Coregonus*, bei der wirklich alles ‚in Fluß‘ ist, überhaupt kaum brauchbar.“

²⁾ This study is one of a group of investigations of the fish of the lakes of the northeastern highlands, Wisconsin, conducted co-operatively by the Wisconsin Geological and Natural History Survey and the United States Bureau of Fisheries.

A similar opinion was expressed by Järvi (1928) who stated: „Die Frage nach den Grenzen zwischen den verschiedenen Coregonenformen wird im allgemeinen als offen betrachtet.“

Still more recently Freidenfelt (1934) observed: „Es ist wohl bekannt, was für ein *crux et scandalon* für den Systematiker die Gattung *Coregonus* seit jeher gebildet hat . . . Zunächst muß daran erinnert werden, daß irgendwelche Arten in herkömmlichem Sinne, d. h. voneinander sicher abgegrenzte, innerhalb der Gattung *Coregonus* nach allem zu urteilen nicht vorkommen. Die Variation aller Arten, Unterarten, Formen — wie man sie nun nennen will — ist mehr oder weniger transgredierend.“

These three observations are but representative of the opinions that have been expressed repeatedly by investigators of the coregonids.

Because the coregonids have not proved amenable to the customary methods of systematic procedure, the matter of the interpretation of the differences among them has been left largely to the personal tastes of the various investigators. The variation in these personal tastes, and the consequent diversity in the methods of approach to systematic studies have resulted in a ruinous lack of coordination between the work of different investigators. Not only does the type of data presented in publications vary widely from one author to another, but two different authors working with closely comparable data may employ almost completely different methods of analysis and arrive at widely differing conclusions. As a consequence carefully executed researches have been so often at cross-purposes that coregonid systematics has been in the paradoxical situation where continued research and publication have increased, not diminished, the confusion surrounding it.

The failure of the great mass of modern investigations to bring about any satisfactory arrangement of the systematics of the coregonids is brought out in a striking manner by the comparison of the opinions of recent authors with the remarks of von Siebold (1863): „Überhaupt sind die Renken- und Felchenarten von den Ichthyologen höchst ungenügend untersucht und beobachtet worden; die meisten haben sich damit begnügt, einzelne Individuen der dem Genus *Coregonus* angehörenden Renken oder Felchen, die sie aus diesem oder jenem See erhalten haben, als besondere Arten hinzustellen, ohne sie vorher genauer mit verwandten Formen aus anderen Fundorten verglichen zu haben. Auf diese Weise ist die Gattung *Coregonus* mit verschiedenen unsicheren Arten belastet, welche die Übersicht der wirklich von der Natur begründeten Arten außerordentlich erschwert, indem zugleich alle jene Abänderungen außer Acht gelassen wurden, welche durch die mannigfaltigen Einflüsse der verschiedenen Seen, in denen die einzelnen *Coregonus*-Arten hier und dort heranwuchsen, bedingt sind.“

Von Siebold mentioned further that he found it difficult to make a ready identification of the three Alpine species „ . . . indem die Profile und Größen-Verhältnisse der einzelnen Körperteile dieser Fische nach Alter und Aufenthaltsort außerordentlich variieren.“ Concerning the probable relationship between the central European coregonids and the more northerly forms, he continued. „Noch schwerer wird es mir aber, wenn ich entscheiden soll, ob die *Coregoni* der alpinen Seen von Mitteleuropa mit gewissen nordischen *Coregonus*-

Formen als Rassen einer und derselben Species zu vereinigen sind oder von denselben als vollkommen spezifisch verschiedene Species getrennt gehalten werden müssen.“

To anyone who is acquainted with the present-day coregonid literature these observations of von Siebold, made more than seventy years ago, must have definitely familiar ring. The most important problems of modern coregonid systematics were well recognized seven decades ago.

The present confusion in coregonid systematics has its origin in an inadequate knowledge both of the scope and nature of the variations of coregonids and of the degree of their plasticity in relation to the nature of their environment. Any classification without the basis of such knowledge is premature and likely to prove artificial³⁾. The artificial nature of much of the coregonid systematics of the past is well demonstrated by the failure of different „systems“ in the light of continued research. The use of the ratios of the various body measurements as diagnostic characters of primary importance has been rather generally discontinued. To-day the classification of coregonids is based chiefly, although by no means entirely, on the number and relative length of the gillrakers. However, the last few years have seen the publication of strong evidence to the effect that even these highly trusted characters may be subject to great modification in the face of changed environment, or may change with growth in a single individual⁴⁾.

Because the systematic methods of the past have tended in general to produce a multiplication of the recognized coregonid forms, and this multiplication of forms has in turn tended to confuse rather than elucidate the relationships within the group, it would appear probable that progress toward a truly natural arrangement of the coregonids will involve a marked diminution rather than an increase in the number of recognized forms. With the elimination of forms that have been named without the basis of real and significant differences and of forms whose differences are of purely environmental origin it may be possible ultimately to determine the true affinities of the various coregonid types. Certain recent researches have thrown such doubt on the validity of the present classification of coregonids as to threaten to reduce the whole problem to an utterly chaotic state. It is probable, however, that these seemingly destructive publications actually represent first real progress toward the solution of a problem that has always proved so baffling to its investigators.

The more recent studies of variation in coregonids have been in general along three different lines: (1) the study of the normal range of variation in the value of characters within a homogeneous sample (including the question of sex diffe-

³⁾ Freidenfelt (1934) expressed a similar opinion when he stated, „Verfrühtes Systematisieren schafft nur künstliche Ordnung und kann den wahren Zusammenhang verschleiern.“

⁴⁾ Prawdin (1929) pointed out that the gillraker number increases with growth in the Maräne, *Coregonus lavaretus lavaretoides*. Freidenfelt (1934) presented strong evidence that the gillraker number may increase with age in *C. amni-petens*, and less convincing evidence for a correlation between relative raker length and body length in *C. oxyrhynchus*.

rences); (2) the study of the nature and magnitude of the changes that take place along with growth; and (3) the study of the nature and magnitude of the changes that occur in response to a changing environment or of the morphological differences that depend upon differences in the nature of the environment.

The lack of adequate knowledge concerning the normal range of variation in coregonids has unquestionably led to unjustifiable separation of forms. With the accumulation of more comprehensive data on the subject it is to be expected that quite a few forms that have been considered distinct will be showed to possess no real differences. Each year sees valuable additions to the available data on the natural range of variation in coregonids.

In the study of the natural range of variation of systematic characters a knowledge of the morphological differences between the sexes is important. Yet much of the systematic work of the past has been done without proper consideration of sex differences in coregonids. Such differences have, however, been showed to exist. Certain recent observations on the question will be mentioned here.

Hart (1931) stated that in the whitefish, *Coregonus clupeaformis*, the males „have larger fins in proportion to their size; males may also have a longer snout proportionally and be less deep.“ Pritchard (1928) and (1931) in his taxonomic study of the genus *Leucichthys* in Lake Ontario observed that the males have relatively longer fins than the females, and noted further that“ . . . in general, the heads of the males are slightly longer than those of females and with them the head measurements, eye, snout and maxillary“. He stated also that „the males are more compressed, and not so deep as the females . . .“. Further study may show that sex differences in certain morphological characters are quite general in the coregonids.

The examination of data without taking into consideration the possibility of differences between the sexes, may therefore lead to an erroneous idea of the population as a whole. The danger of such errors is the greater if the samples used for systematic study are taken from a spawning run, for it has been observed repeatedly that the sex ratio in spawning run samples does not represent the ratio of the natural population, and further that the sex ratio varies from one time of the spawning season to another. It should be mentioned also that the sex ratio is subject to wide changes with increase in age (Hile, 1936) and hence that the average obtained for a body ratio with respect to which a sex difference exists may depend in part on the age and size composition of the sample.

Failure to take into consideration the changes in body proportions with growth offers even greater dangers than the neglect of sex differences. Differential growth of the part with respect to the whole appears to be characteristic of the coregonids. Von Siebold (see direct quotation, page 4) mentioned the change of body proportions with increased age as a serious impediment to the separation of the alpine species. Nüsslin (1882) in a detailed discussion of the problem showed that other earlier ichthyologists had been well acquainted with the phenomenon. Later investigators have mentioned frequently the change of body form with growth.

In spite of the almost universal recognition of the existence of differential growth of the body parts in coregonids, the available data on the subject are

on the whole scattered and poorly organized. Thoroughgoing analytical studies are in general lacking. The recent work by Freidenfelt (1934) represents a new departure in the method of study of coregonid variation in this respect. Freidenfelt included not only observational data on the change of morphological characters with growth, but also subjected these data to detailed mathematical analysis to determine the exact significance of the observed changes. Further studies of this type should contribute much toward a better understanding of variation in coregonids.

Much research on the relationship between environment and morphological characters has been done on certain species of fish other than coregonids. These studies have included investigations of natural populations as well as experimental work. Meristic characters appear to be particularly sensitive to such environmental factors as temperature and salinity. (Hubbs, 1926) interpreted the effect of environment on meristic characters as operative through a control of the rate of development.) These numerous researches on the modifying effects of environment on fish, however, are generally well known and do not need to be reviewed at this time. A review of the subject may be found in Hubb's (1934) publication.

The difficulty of rearing coregonids beyond the fry stage in aquaria or ponds has unfortunately served as a most serious obstacle to any detailed experimental investigation of the direct effect of the environment on the morphological characters of this group. Although artificial rearing of coregonids succeeded in some cases, these artificially reared fish usually show a distinct tendency to be abnormal in appearance (Koelz, 1929, Freidenfelt, 1934).

Because of the aforementioned difficulty of direct experimentation, data bearing on the question of the direct effect of environmental conditions on the anatomical characters of coregonids have been derived chiefly from the observation of parallelisms between differences in certain environmental factors and differences with respect to certain morphological characters, and also from the observation of changes in body structure that have occurred when a stock has been transplanted into a new locality.

In the American coregonids there have been several observations of parallelism between environmental factors and structural characters.

Dymond (1926) stated that all species of *Leucichthys* taken from Ombabika Bay (Lake Nipigon) had a larger eye than fish of the same species taken in the main body of the lake. Dymond and Hart (1927) showed that *Leucichthys nipigon* of Lake Abitibi, an exceptionally shallow body of water, „has a deeper and more compressed body than is found in the same species in Lake Nipigon. The Abitibi form also shows fewer scales, longer fins, and a shorter, stouter caudal peduncle.“ These authors called attention further to the fact that the whitefish, *Coregonus clupeaformis*, of the two lakes show „exactly parallel“ differences.

In his study of the Coregonidae of the Great Lakes, Koelz (1929) observed that the deep water forms of *Leucichthys hoyi* are characterized by relatively longer heads, longer paired fins (especially the ventrals), and longer mandibles than the shallow water forms. Koelz also mentioned the relatively long mandible of the race of *Leucichthys artedi* occupying the deeper (eastern) portion of Lake Erie. Correlations exist also between certain morphological characteristics and

temperature. The *manitoulinus* and *albus* forms of *L. artedi* are both characterized by " . . . deep abbreviated bodies, . . . relatively long paired fins, and few lateral line scales", and both „always occur in the warmest waters of the territory available for occupation“. Koelz found that warm water forms of *Coregonus clupeaformis* are also characterized by deeper bodies and fewer lateral line scales than cold water forms. Koelz held, however, „that facts do not warrant the assignment of temperature as a direct factor in occasioning the variations discussed.“

Hart (1931) reported that in Lake Ontario, whitefish taken in increasingly greater depths of water „show a decrease in proportionate depth of body and proportionate length of fins.“ He called attention to the parallel situations in Abitibi and Nipigon, and concluded, „The evidence cited lends credibility to the belief that considerable differences in body proportions of whitefish may be due to differences in environment and that one of the environmental factors producing such differences is depth of water.“

Bajkov (1933) in his comparison of *Coregonus atikameg* (an anadromous species from Hudson Bay) with its freshwater form, *C. atikameg manitobensis*, observed that the relationship between the two is paralleled by the anadromous and freshwater forms of Siberia.

Similar parallelisms have been observed by European investigators. One of these observations, because of the lively interest it excited among coregonid systematists, should be mentioned here. In his study of *Coregonus lavaretus* in Denmark, Otterstrøm (1922) observed that the various populations fall into the following general groupings with respect to the number of gillrakers on the first branchial arch:

34 gillrakers or more — freshwater forms.

32,5 gillrakers or less — brackish water (fjord) forms.

The two groups show further the usual relationship that the lesser number of gillrakers (in the brackish water populations) is associated with a lesser relative length of gillrakers. Otterstrøm observed also that in almost all cases where the brackish water form (Snaebel) is found in the fjords or in the brackish water area before river mouths a population of the freshwater form (Helt) is found in the river, and that the relative abundance of „Helt“ and „Snaebel“ depends on the extent of the brackish water area available to the latter type. On the basis of his researches Otterstrøm concluded that „Helt“ and „Snaebel“ do not form separate stocks, but that the „Snaebel“ is to be considered as an element of the „Helt“ population living in brackish water. Otterstrøm pointed out that while the differences in gillraker structure appear to vary according to the salt content of the water, it need not be considered that salinity is the direct and determining factor. It is possible, for example, that salinity may produce structural differences indirectly through the modification of feeding habits.

The most convincing arguments for the great plasticity of coregonids in the face of changes in environmental conditions appear from the observation of morphological changes that have resulted from the transplantation of stocks from one locality to another. The activities of European pisciculturists in transplanting the coregonid forms from one lake to another for the purpose of rehabili-

tating depleted stocks, and in introducing coregonids into lakes that were originally not inhabited by them, have made possible the conduct of numerous „experiments in nature“.

In 1912 Thienemann published the details of the unusual results of his investigations of the „Silberfelchen“ or „silver whitefish“ of the Laacher See. This lake, which lies in the crater of an extinct volcano, possessed no autochthonous population of coregonids. Nevertheless Thienemann found that the specimens he examined from the lake corresponded to no known form of coregonid, either of the Alpine lakes or of North Germany. From the examination of the available records concerning the planting of coregonid eggs in the lake, and from the comparison of the Laacher See form with those coregonids which might possibly have constituted the parental stock, Thienemann concluded that the Laacher See silver whitefish most probably originated from introductions of *Coregonus fera* from the Bodensee in 1866 and 1872. The Laacher See fish differed from *C. fera* of Bodensee in three important respects: (1) the yellow pigment characteristic of the Bodensee larvae was completely lacking in the larvae from the Laacher See; (2) the characteristic numbers of the gillrakers on the arches, I to IV, respectively are in *fera* 23 — 25 — 22 — 19, while in the Laacher See form they were 44 — 46 — 40 — 32; (3) the relationship of the length of the gill arch to the length of the longest gillraker in the Bodensee and Laacher See forms respectively was for arch I, 5.9 and 3.7, and for arch II, 11.4 and 7.3.

Thienemann held that these changes took place since the planting of *C. fera* in Laacher See, and that they are of such a nature that it is possible to speak of the very recent origin of a new species in that lake. While the changes described show a logical relationship with a transfer to the very transparent water of the Laacher See, and with a change from bottom feeding to a plankton diet the mechanism for the changes presents a troublesome problem. The amount of time between the introduction of coregonids into the lake and Thienemann's examination of the population (only about seven generations) was so short that selection in the Darwinian sense fails to offer a satisfactory solution. Thienemann could not be definite as to the causes of the changes, but merely held them to be the result of „... die äußeren Milieubedingungen ... im Verein mit inneren, historisch begründeten und gewordenen Entwicklungstendenzen ...“.

In an addendum to the publication Thienemann stated that the Laacher See coregonid planted in a nearby quarry retained its resemblance to the parent form both as to external appearance and structure of the gillrakers.

In a later publication Thienemann (1915) reaffirmed his previous stand on the question of the Laacher See whitefish and presented data to show that 60 young reared to their third summer in ponds agreed in structure with the parent stock. Thienemann's belief that the Laacher See coregonid represents a real and distinct form is apparent from the fact that in his general grouping of European coregonids (Thienemann, 1921) he included it under the name of *fera Sancti Benedicti* in the *Wartmanni-generosus* group (members of this group have an average gillraker number of 35 to 53—54 on arch I, while he included the supposed parent stock, *C. fera* in the *Fera-Holsatus* group (average number of gillrakers on arch I, 19—25). In his 1921 paper Thienemann suggested that mutation may have played a rôle in the origin of the Laacher See fish.

Wagler (1927) and Bauer (1927) objected to Thienemann's interpretation of his findings concerning the „Silberfelchen“ of the Laacher See. The former author held that the parent stock of the Laacher See coregonid was *C. macrophthalmus* and not *C. fera* since, he contended, Thienemann's description for the Laacher See fish fitted *C. macrophthalmus* quite well. Bauer disagreed with Wagler's conclusions, and held that the Laacher See coregonid and *C. macrophthalmus* can not be included under the same description. He expressed the opinion that the parent stock of the Laacher See coregonid is some, as yet undetermined, „Kleinrenke“ population from a Swiss Lake. Surbeck (1927) also opposed Wagler's ideas but, contrary to Bauer, showed sympathy with Thienemann's original interpretation. Thienemann (1928) mentioned Wagler's statements and pointed to Surbeck's and Bauer's opposition to them. In the same paper he offered a refutation of Bauer's (1927) criticisms.

Surbeck's (1921) observations on the effect of change in environment on the gillraker number of *C. Schinzii helveticus* Fatio of Vierwaldstätter See offer a second example of the apparently great plasticity of coregonids with respect to this character. Shortly after 1900 the Vierwaldstätter See stock of the „Balchen“ declined almost to the point of commercial extinction. Beginning in 1911 remedial measures were taken in the form of large introductions of coregonid fry from Sempachersee. The effects of these plantings were noticeable in a very few years, and by 1918 and 1919 the commercial fishery had again become important. The catch of this restored fishery contained two types of individuals which the fishermen considered to represent the „old, native“ form and the introduced „Sempacher“ form.

Surbeck found from his examination of specimens from the Vierwaldstätter See that the individuals of the two groups could be separated readily at first glance. The „Sempach“ individuals were distinguishable not only by their slender body form but also by a much darker pigmentation of the dorsal region. Data on the body proportions supported these conclusions as to the presence of two types of coregonids in the lake. The study of the gillrakers, however, failed to reveal differences between the two groups with respect to this character, for the „old“ form had 24—26 and 21 gillrakers on the first and fourth arches, respectively, while the corresponding numbers for the „Sempach“ form were 23—25 gillrakers on the first arch and 21 gillrakers on the fourth. The data for both forms conformed closely with Fatio's (1890) description of *Coregonus Schinzii helveticus* (23—28 gillrakers on the first arch and 21—22 gillrakers on the fourth).

In order to compare the „Sempach“ individuals of Vierwaldstätter See, with the supposed parental stock, Surbeck examined coregonids taken directly from Sempacher See. These latter individuals had 30—36 gillrakers on the first arch and 25—28 gillrakers on the fourth. Thus Surbeck found that the Sempacher See coregonid differed widely from the „Sempach“ form of Vierwaldstätter See. The data for the Sempacher See coregonid, however, failed to agree with Fatio's (1890) description of the coregonid in that lake, for Fatio assigned the Sempacher See fish to the species, *C. suidteri*, characterized by 38—42 gillrakers on the first arch and 24—28 gillrakers on the fourth.

Surbeck explained the disagreement between his and Fatio's descriptions

of the Sempacher See coregonid on the basis of introductions of *C. Schinzii helveticus* from Vierwaldstätter See into Sempacher See subsequent to Fatio's description of the coregonid of the latter lake. In the early nineties the coregonid stock of Sempacher See was badly depleted, and as a consequence the years 1895—1902 saw the introduction of large quantities of fry from the then well populated Vierwaldstätter See. These introductions were successful in restoring the abundance of the Sempacher See stock. Surbeck concluded, therefore, that the „Balchen“ stock of Sempacher See that provided young for the recent plantings in Vierwaldstätter See was not *C. soidteri* as described by Fatio but was composed of descendants of the earlier (1895—1902) plantings of *C. Schinzii helveticus* from Vierwaldstätter See. This conclusion is supported by the observations of the Sempacher See fishermen that following the introduction of Vierwaldstätter See young the Sempacher See fish came to resemble the Vierwaldstätter See type both as to appearance and size. On the basis of these several considerations Surbeck held that *Coregonus Schinzii helveticus*, upon transfer in 1895—1902 from Vierwaldstätter See to Sempacher See, changed its gillraker number from 24—26 gillrakers on the first arch and 21 gillrakers on the fourth to 30—36 gillrakers on the first arch and 25—28 gillrakers on the fourth, and that a subsequent return to the Vierwaldstätter See environment was accompanied by a reversion to the ancestral type in gillraker numbers. Surbeck further pointed out that the observed changes can not be explained satisfactorily on the basis of hybridization between native and introduced stocks, since it can not well be assumed that such hybridization would be universal. Consequently some non-hybrid individuals with the characteristic low gillraker number of *C. Schinzii helveticus* would be expected to occur in Sempacher See or individuals with high raker numbers would be expected to occur in Vierwaldstätter See. Surbeck, however, found no such „pure“ individuals in either stock.

Kulmatycki (1926) in his study of the coregonids of Poland pointed out that young of the marena or „Große Maräne“ (*C. lavaretus* L.⁵) of the Putziger Wiek (Gulf of Danzig), when reared in fresh water have a much greater height of the dorsal fin than is showed by the parent stock in its native brackish-water habitat, and tend rather to assume the fin size typical of freshwater forms.

In the same publication Kulmatycki called attention to the problem presented by the marena of the Wielkie Okonińskie See. Although this coregonid is an introduced form there is no absolute certainty concerning its origin. There is, however, strong evidence that it may have originated from plantings of the „Blaufelchen“ or blue whitefish (*C. Wartmanni*) of upper Bavaria. The Wielkie Okonińskie fish, nevertheless, has both the appearance and the habits of *C. lavaretus*.

Kreitmann (1929) described the morphological changes which he believed the lavaret, *C. (dispersus) Wartmanni lavaretus* Fatio, underwent when it was transferred from Le Bourget to Le Leman. Each of these lakes possesses two

⁵ In the earlier classifications of the „Große Maräne“ the Putziger Wiek form would, because of its low gillraker count, fall within the species *C. holsatus*. Kulmatycki, however, interpreted all Polish „Große Maräne“ as forms under the single species, *C. lavaretus* L.

autochthonous forms of coregonids. In Le Lemane they are the „gravenche“, *C. (balleus) hiemalis* and the „fera“, *C. (balleus) Schinzii fera*. In Le Bourget there occurs in addition to the lavaret the form, *C. (balleus) hezola* Fatio. According to Kreitmann these forms show the following number of gillrakers on the first and fourth branchial arches:

Form	<i>C. lavaretus</i>	<i>C. hezola</i>	<i>C. hiemalis</i>	<i>C. fera</i>
Arch I	32—38	31	25—29	23—27
Arch IV . . .	25—28	24	17—23	15—19

The lavaret is a member of Fatio's *dispersus* group which is characterized by numerous and relatively long gillrakers and a terminal or quasi-terminal position of the mouth. The other three forms belong to Fatio's *balleus* group in which the gillrakers are few and relatively short and the mouth is inferior or „pre-inferior“.

The occasion for the introduction of the lavaret into Le Lemane was a continuous decline of the yield of the coregonid fishery in that lake—a decline that brought a once prosperous fishery to the point of practical extinction. Since the small catch of the native stock could not furnish sufficient spawn for purposes of artificial propagation, it was found necessary to stock the lake with the young of some other coregonid population. For this purpose the lavaret of Le Bourget was selected. During the period 1922—1925 approximately eight million fry were introduced into Le Lemane. Two years after the first planting there occurred a distinct upturn in the catch of coregonids in Le Lemane. The catch of 1924 was four times as great as that of 1923, and the 1925 catch was twenty times that of 1923. The catches included great numbers of fish that showed themselves to be lavarets on the basis of their body form, color, length of fins, profile of the head, position of the mouth, and quality of flesh. With respect to the number of gillrakers, however, they differed widely from the parent lavaret stock. The lavaret of Le Bourget had 32—38 gillrakers on the first arch and 25—28 on the fourth; in the Le Lemane form these numbers were 24—28 and 17—21 respectively. These values show a close resemblance to those for *C. fera*. Thus there is strong evidence that in one generation *C. lavaretus*, on the basis of gillraker counts, may have changed from the *dispersus* to the *balleus* group of coregonids.

Kreitmann found further evidence of the plasticity of the lavaret in his examination of that form from the lac d'Aiguebelette. This body of water had also been stocked with young from Le Bourget, but here the gillraker numbers were observed to increase from 32—38 to 39—41 on the first arch and from 25—28 to 33—35 on the fourth.

As a final argument for the close relationship of the coregonids of the different lakes Kreitmann showed that eggs of the „lavaret“ fertilized with sperm from the „gravenche“ gave as high a percentage of embryos as is ordinarily obtained in the artificial propagation of the coregonids. On the basis of his observations and those of other investigators Kreitmann concluded that, „... il semble illusoire de chercher à compartimenter, les Corégones en espèces ou en sous-espèces.“

In a later paper (Kreitmann, 1931), the same author reviewed the recent work of several investigators of the problem of the variability and the plasticity of the various coregonid forms. The nature of his conclusions appears in the following quotation: „... ces affinités sont assez étroites pour qu'il devienne impossible de diagnostiquer un Corégone autrement que par l'habitat dont l'influence devient prépondérante pour imprimer au Corégone sa marque; celle-ci n'est d'ailleurs par définitive et se plie à de nouvelles conditions d'habitat . . . L'on arrive ainsi en conclusion à ne plus considérer les manifestations de Corégones dans notre continent, si variables, si interchangeables, si étroitement liées à l'habitat que comme des formes locales d'une espèce dont la variabilité même doit lui faire attribuer dénomination de *C. mutabilis*.“

The views of Kreitmann find full support in the investigations of Monti (1929, 1930, 1933) who, with the assistance of Stolz and Perotti, studied the coregonids of the lakes of northern Italy. None of the Italian lakes contain autochthonous forms of coregonids. The first introduction of coregonids into Italian lakes was made by Pavesi in lakes Lario and Verbano in 1880 with eggs obtained directly from Lake Constance (Bodensee). New introductions followed during the ensuing years. After the coregonid was established in Italy the various local stocks served as a basis for introductions into yet other lakes. According to Monti the following recognized forms were imported into Italy:

1. *C. Wartmanni coeruleus* Fatio from Lake Constance — coregono azzuro, lavaretto, corégone lavaret, Blaufelchen.
2. *C. Schinzii helveticus* Fatio var. *bodensis* Fatio from Lake Constance and var. *zugensis* Fatio from Lake Zug — coregono bianco, Sandfelchen, Weißfelchen.
3. *C. maraena* Bloch from the large ponds of Wittingau in Bohemia — coregono marena, Maräne.

Monti, after extensive researches into the morphometry and the biology of the Italian coregonids, concluded that under the influence of changed environments, they had become modified into a number of diverse forms each one characteristic of the basin it inhabited⁶⁾. She further concluded that: (1) the particular appearance of each of the local forms seems to depend on the specific nature of the local environment; (2) any resemblance that a population may happen to bear to one of the original ancestral stocks is of little significance as such resemblance may disappear completely if the form is introduced into yet another environment; and (3) the various characters have showed themselves to be modifiable and reversible according to changes in the environment.

The cytological investigations of Italian coregonid stocks (Monti, 1933) furnished further evidence for their genetic unity. In all of the various populations the diploid number of chromosomes was determined as 24. Neither did there appear any detectable differences among the populations as to size and shape of the individual chromosomes.

⁶⁾ „... adattandosi nei singoli bacini dove vennero importati, si sono frantumati in una serie di forme diverse fra loro, ciascuna propria di ciascun bacino e persistenti nel loro abito morfologico finchè perdura l'ambiente.“ (Monti, 1933.)

Monti found it possible to show a connection between certain of the modifications observed in the Italian coregonids and certain factors in the environment. The bluish color was found to be characteristic of the forms occurring in the deep expanses of the larger lakes while the forms living in shallow littoral regions were found to be white or brownish-white. The shallow water forms showed a greater proportionate depth of body (cf. Dymond and Hart [1927] and Hart [1931]). In wide deep lakes the head was small and elongate while in shallow areas the head was relatively heavier and deeper. The position of the mouth was found to be related to feeding habits; in the planktophagous forms its location was terminal and in the bottom feeders it was inferior. The gillraker number, according to Monti, likewise showed correlation with feeding habits. The number on the first arch varied from 29—31 in the plankton-eating forms from lakes Lario, Verbano and Benaco to 23—24 in the bottom feeding forms of lakes Bracciano and Bolsena. Growth appeared to be quite variable from lake to lake and dependent on feeding conditions, although in general, growth was superior to that of the ancestral stocks in the transalpine lakes, and sexual maturity was reached at an earlier age.

Monti concluded that only one species of coregonid exists in Italy and identified it with *C. lavaretus* L. She considered the various local forms to be purely of environmental origin and termed them „nations“. The significance of her final conclusions⁷⁾ is very similar to that of Kreitmann's.

These various observations on the effect of transplantation to a new environment on the morphological characters of coregonids tend to substantiate much that has been suspected. They are contributions of tremendous and fundamental importance. It would be highly desirable, nevertheless, to have available the results of transplantation experiments whose antecedents are so perfectly known that there can be no room for skepticism concerning the reliability of the conclusions based upon them. Such future experiments should seek to avoid any possibility of the confusion of the introduced fish with autochthonous forms, of uncertainty as to what form was introduced, or of the obscuring of the results through the hybridization of two or more forms.

Although the artificial propagation of coregonids has been carried on in America for several decades there are few data on the effect of change of environment on the morphological characteristics of transplanted fish. In 1929 Koelz compared the morphological characteristics of the Great Lakes whitefish (*Coregonus clupeaformis*) with those of 32 specimens of Lake Erie parentage, reared artificially in the New York Aquarium. His data showed that the head, eye, maxillary, snout, and paired fins were relatively much longer in the artificially reared fish than in the Great Lakes stocks. The artificially reared fish also showed a reduced number of gillrakers on the first arch — 25,3 as compared with 27,3 in the Great Lakes. Koelz described the differences in body form between artificially reared whitefish and Great Lakes populations as follows: „The body

⁷⁾ „... in Italia esiste una *sola unica specie*, frammentata in tante forme locali le quali hanno assunto caratteri propri, ma ancora modificabili e reversibili — e perciò non hanno ragione di ricevere una particolare classifica che potrebbe far pensare a sotto-specie, varietà costanti o razze ben distinte“ (Monti, 1933).

parts show great modification in all the specimens, and none of them resemble any whitefish taken in the Great Lakes. The most striking differences are changes in the shape of head parts. The head throughout is much deeper than in normal whitefish, and its dorsal contour usually is decurved conspicuously anterior to the orbit . . . The premaxillaries are often vertical in position, which is not known to be the case in normally reared individuals. The head is broader, especially across the snout, and the adipose is much larger usually."

In a later publication (Koelz, 1931) the same author mentioned a brood of whitefish reared artificially by the Ontario (Canada) Game and Fisheries Department, and stated that these fish „duplicated exactly“ the results of the New York Aquarium experiment.

Greeley (1934) mentioned the wide variation in the body proportions of the whitefish (*C. clupeaformis*) in the lakes of the Adirondack region, New York. Concerning the causes of these differences he stated: „Since the common whitefish of the Adirondack region was probably introduced from the same stock (Saranac Hatchery) the differences in body proportions of the fish from various lakes are of interest as indicative of direct effect of environmental conditions."

Not all transplantations of coregonids have resulted in such striking indications of the plasticity of the groups as those just described. Some, on the contrary, have yielded evidence for a high degree of constancy for certain characters at least. Surbeck's (1917) examination of a single specimen from Aegerisee indicated a close agreement in gillraker number between the introduced stock and the Zugersee „Balchen“ (*Coregonus Schinzii helveticus*), one of the coregonid forms that had been planted in previous years. Thienenann (1921) mentioned Surbeck's observations and presented three other examples in which populations of transplanted coregonids retained the characteristics of the parent stock, even over long periods of time. Järvi (1928) found the gillraker structure of the „Murole marena“ (*C. generosus* Peters f. *aspia* Smitt) to show very close agreement with that of the ancestral stock from Eura — Pyhäjärvi. Certain differences between the two stocks in the proportions of the head he attributed to the difference in the age composition of the samples for which the comparisons were made. Similarly Mannsfeld (1930) found close agreement between the Burtnecker See marena and the parent form of the Peipussee.

An example of an apparently high degree of constancy in an American coregonid is afforded by the transplantation of the Lake Erie cisco, *Leucichthys artedii albus*, to the Wisconsin waters of Lake Michigan⁸). In the autumn of 1924 several million cisco eggs were obtained from the Canadian shore of Lake Erie and transported to Wisconsin. Half of them were planted at once in the Lake Michigan waters off Port Washington, while the remainder were retained in state hatcheries and planted in the same locality as fry the following spring. In the autumn of 1930 Port Washington fishermen took several fish that gave every appearance of being Lake Erie ciscoes. That this resemblance to the

⁸) The data concerning the results of this transplantation were provided by Dr. John Van Oosten. In Charge of Great Lakes Investigations of the Bureau of Fisheries, and are published here with his kind consent.

Lake Erie cisco extended to the quality of the flesh was demonstrated by smoking tests made by commercial fishermen on several individuals. A single specimen of these „Erie ciscoes“ of Lake Michigan waters was sent to the Great Lakes laboratories of the Bureau of Fisheries. The results of the examination of this individual are summarized in the following quotation from Dr. John Van Oosten's report (unpublished) for the month of November, 1930. „On examination this specimen showed the typical taxonomic characters of the Lake Erie cisco, *Leucichthys artedi albus* . . . An examination of the scales revealed five annuli or winter-rings and this fish was therefore in its sixth summer. This indicates that the specimen was one of those planted by Mr. Smith in the fall of 1924 or in the spring of 1925.“

The preceding brief review of some of the more recent literature on the problems of the nature of variation in coregonids and of their plasticity in the face of changed environment should be sufficient to show the trend in the present-day investigations of the group. One after another the lines of demarcation which have served to separate the various species appear to be breaking down. When it seemed that the use of body proportions was not yielding reliable results in the systematics of the group, more and more dependence came to be placed in the divisions based upon the number and relative length of the gillrakers. The rapidly accumulating evidence for the sensitivity of the gillraker characters to the conditions of environment bids fair to leave the coregonids without any diagnostic character of certain worth. Accordingly several European investigators are being forced to the conclusion that many forms that in the past have been designated as species and subspecies must be recognized as nothing more than the direct products of the local environment operating on an inherently highly plastic form.

The systematics of the North American coregonids appears to be in a state of confusion closely comparable to that which has existed in Europe. It will be interesting to observe what clarification will result from the conduct of investigations to determine the true range of variability and the actual degree of plasticity of the coregonids on this continent. It is not unreasonable to expect that many of the subspecies and even some of the species that are recognized at the present time may later be relegated to the category of ecological variants or environmental forms.

Growth of the cisco in Trout Lake, Muskellunge Lake, Silver Lake, and Clear Lake.

Since the question of the relationship between growth rate and certain morphological characteristics constitutes one of the most important phases of the present study of the morphometry of the cisco, a short summary of the growth history of each of the four populations, together with a brief consideration of certain growth relationships will now be presented. Tables 2 and 3 show the growth histories of the four stocks with respect to growth in length and growth in weight, respectively.

The lengths in Table 2 are the average calculated standard⁸⁾ lengths in millimeters at the end of each year of life. These lengths were calculated from the measurements of the diameters of the successive growth areas of the scales. The computations were based on the assumption that the ratio of scale diameter to body length is constant for all lengths of fish beyond that at which the first annulus is laid down. It may be seen that the order of the lakes with respect to the growth rate (in length) of their cisco populations, from minimum to maximum, is: Trout Lake, Silver Lake, Muskellunge Lake, Clear Lake.

Table 3 shows the average weight in grams of the different age groups at the time of their capture in the summer, during the growing season. Here the order of the lakes with respect to the growth rate of their cisco populations, from minimum to maximum, is: Trout Lake, Muskellunge Lake, Silver Lake, Clear Lake.

From Tables 2 and 3 it may be seen that, while the Muskellunge Lake cisco has the more rapid growth in length, the Silver Lake cisco, by reason of its more robust form, has the more rapid growth in weight. Whether the Silver Lake cisco or the Muskellunge Lake cisco is actually considered to have the more rapid growth depends on the point of view. If growth is considered in terms of the amount of living matter produced, the Silver Lake cisco with its more rapid growth in weight must be recognized to show better growth than the Muskellunge Lake cisco. On the other hand it might be argued that, from the viewpoint of morphometric studies, the more rapid growth of the Muskellunge Lake cisco along the antero-posterior axis is more significant than the superior growth in weight of the Silver Lake cisco, for many of

⁸⁾ Standard length is measured from the tip of the snout to the base of the caudal peduncle.

the body ratios employed in morphometric studies are based on measurements of body parts along this antero-posterior axis and would not be affected by the individual heaviness of build.

Among the more important relationships brought out in the previous study of the growth of the cisco populations of Trout Lake, Muskellunge Lake, Silver Lake, and Clear Lake, are the following:

(1) The order of the four populations with respect to rate of growth in weight is the reverse of their order with respect to the density of the populations; that is, a greater population density makes for a poorer rate of growth.

(2) With the exception of the interchanged positions of the closely similar Muskellunge Lake and Silver Lake populations the order of the four lakes with respect to the densities of their cisco populations is the reverse of their order with respect to the abundance of bound CO_2 in their waters. Thus the lake with the softest water (Clear Lake) has the sparsest but fastest growing cisco population, while the lake with the hardest water (Trout Lake) has the most dense but slowest growing population of ciscoes.

(3) The length of the growing season of the cisco varies from a minimum of about three months in Trout Lake to a maximum of approximately five months in Clear Lake. The four lakes follow the same order with respect to the length of the growing season of their cisco populations as they follow with respect to the rate of growth in weight. However, differences from lake to lake in the length of the cisco's growing season fail to account entirely for the observed differences in growth rate. Although the causes of the variations in the length of the cisco's growing season in different lakes are not known, it is certain that they do not depend on differences in water temperature.

(4) The order of the four lakes with respect to the sex ratio (number of females per 100 males) is the reverse of their order with respect to growth in weight; that is, slow growth is correlated with a higher relative mortality of the males and consequently a greater relative abundance of females.

(5) The average condition of the four cisco populations (as estimated from the value of K in the equation, $\text{Weight} = K \times \text{length}^3$) from minimum to maximum followed the order: Muskellunge Lake, Trout Lake, Silver Lake, Clear Lake. This is the reverse of the order of the lakes with respect to the abundance of organic matter in the plankton.

In Muskellunge Lake and Trout Lake the cisco grows more slender as it increases in length, while in Silver Lake and Clear Lake it becomes more robust with increase in length.

(6) The order of the four populations with respect to average longevity is the same as their order with respect to condition, that is, a high value of K is associated with a relatively long life.

From the preceding brief review of the growth relationships in the cisco it is apparent that differences in the life histories of various cisco populations are intimately associated with differences in certain environmental factors. The sections to follow will be concerned largely with the question of the extent to which environmental conditions may affect also the morphological characteristics of the cisco. Particular attention will be given to the modifying effects of environmental conditions as they operate through the control of the rate of growth.

Materials and methods for the morphometric studies.

This investigation is based on 1,548 specimens collected in July, August, and early September of 1931 and 1932. Table 4 shows the age and sex composition of the material used in the general investigation of the morphometry of the four cisco populations. The ages designate the number of annuli on the scales, or the number of years of life completed. The 795 specimens taken from Muskellunge Lake in 1932 were collected for a special study of the differences between the 1928 and 1929 year classes of that population (see page 52), and hence are not included in the table. In the general study of the morphometry of the four populations the individuals whose age could not be determined were excluded in the compilation of the morphometric data. The examination of the data for these discarded fish, which composed less than five per cent of the total samples, showed that their exclusion did not affect the results obtained for the different populations.

With the exception of seventeen O-group individuals picked up along the beaches of Trout Lake, all specimens were taken by means of gillnets. The sizes of mesh used were (stretched measure, in inches): $1\frac{1}{4}$, $1\frac{1}{2}$, $1\frac{3}{4}$, 2, $2\frac{1}{4}$, $2\frac{1}{2}$, and 3.

The specimens were held in a solution of ten per cent formalin until the close of the collecting season. They were then removed from this solution, permitted to soak in water for two or three days, and transferred permanently to a seventy per cent solution of alcohol. The

shrinkage in length caused by the preserving fluids up to the time when the specimens had been in alcohol approximately five weeks was, on the average, slightly less than two per cent (Hile, 1936).

Some consideration should be given to the various sources of error in the conduct of a morphometric study. It is probable that the relative amount of shrinkage produced by the preserving fluids varies in different parts of the body. The measurements used in this investigation were taken from preserved fish, and the ratios calculated from them may be expected to differ slightly from those based upon measurements of fresh fish. However, all fish employed in this study were preserved by the same method, and it appears altogether unlikely that the differential shrinkage of the different parts of the body would vary sufficiently from lake to lake to have any effect on the comparisons of corresponding body ratios.

Measurements of the body parts were made by the use of dividers, and their values read from a millimeter ruler. These measurements were recorded to the nearest half millimeter. There was, however, a noticeable tendency, particularly in the longer measurements, to read to the full millimeter more frequently than to the half millimeter. In spite of the care that was taken to make the procedure uniform throughout the investigation it is probable that there were slight differences from day to day in the method of making the various measurements. These personal errors no doubt tend to compensate each other, and may be assumed to have no effect on the general results. The effect of such daily differences in procedure is lessened further by the fact that the fish were measured in an indiscriminate order without respect to size.

All measurements and counts were made by the same person, Mr. William Duden, formerly research assistant in the Bureau of Fisheries. Thus there is no question of errors arising from differences of procedure of two or more investigators.

The following measurements and counts were made on each specimen in the general study of the morphometry of the four stocks:

Length (L). From the anterior tip of the premaxillaries to the end of the last vertebra.

Length of head (H). From the anterior tip of the premaxillaries to the extreme posterior margin of the opercular membrane.

Snout (S). From the anterior tip of the premaxillaries to the anterior bony margin of the orbit. In making this measurement the tip of the dividers was inserted into the eye socket.

Eye (E). Antero-posterior diameter. The dividers were inserted into the orbit and brought into contact with the eye at its greatest diameter. Care was taken not to compress the eye-ball.

Interorbital (I). The least distance between the bony margins of the inter-orbital. This measurement was made only on the Muskellunge Lake specimens.

Length of pectoral fin (P), and of *ventral fin* (V). From the insertion of the fin to the tip of its longest ray.

Length of adipose fin (AD). From origin of fin to its distal end.

Base of dorsal fin (DB), and of *anal fin* (AN). The length of the fin base, measured along the body.

Dorsal height (DH). The length of the longest ray in the dorsal fin.

Pectoral-ventral distance (PV). From the insertion of the pectoral fin to the insertion of the ventral fin.

Ventral-anal distance (AV). From the insertion of the ventral fin to the origin of the anal fin.

Maxillary (M). From the anterior tip of the premaxillaries to the posterior end of the maxillary bone.

Depth (D). The greatest vertical depth of the body.

Width (W). The greatest width of the body.

Adipose-caudal distance (AT). From the origin of the adipose fin to the first rudimentary caudal ray on the upper edge of the caudal fin.

Depth of the caudal peduncle (DCP). The least vertical depth of the peduncle.

Gillrakers (R). Every visible gillraker on the first branchial arch. The arch was removed carefully with a sharp scalpel, cleaned and held completely spread, to facilitate the counting of the rakers.

Lateral line scales (Sc). All the perforate scales of the lateral line. When the scales were lost the scale pockets were counted.

Dorsal scale rows (RD). The number of scale rows from the middle of the base of the dorsal fin to but not including the lateral line row.

Peduncle scale rows (RC). The number of scale rows around the entire circumference of the peduncle, at the point of its least depth.

Branchiostegal rays (BR). Every ray in the opercular membrane.

Fin rays: dorsal (DR); *anal* (AR); *pectoral* (PR); *ventral* (VR). Total number of rays, except the „rudimentary“ rays in the dorsal and anal fins. Those rays which did not extend to the tip or nearly to the tip of the fin were not included in the count.

Measurements and counts were ordinarily taken from the left side of the body. When, exceptionally, some injury to the specimen made this procedure impossible, the right side of the body was used.

The following body ratios were calculated for each individual in all but the 1932 Muskellunge Lake collections; L/H, L/D, L/W, L/AT, L/DCP, L/DB, L/AN, L/AD, L/PV, L/E, PV/AV, H/S, H/E, H/M, D/E, PV/P, AV/V, DH/DB. The ratio H/I was computed only for the Muskellunge Lake ciscoes. In the 1932 Muskellunge Lake collections the following measurements were taken: L, H, D, DCP, E, and I. From these measurements were calculated the ratios: L/H, L/D, L/DCP, L/E, H/E, H/I. Since the samples obtained from Muskellunge

Lake in 1932 were taken for a special purpose and treated in a special manner, they will be considered separately from the remaining collections.

In the analysis of the morphometric data the specimens from each population were divided into groups on the basis of sex, age, and length. Combinations of these original groupings were made as far as the examination of the data appeared to justify the procedure. The materials presented in the sections that follow represent largely such summarizations. The results of the more detailed analysis will be presented only when the consideration of details appears necessary to a proper understanding of the significance of the data.

Comparison of the morphological characteristics of the cisco populations of Trout Lake, Muskellunge Lake, Silver Lake, and Clear Lake.

In this section will be presented data to show the differences among the four cisco populations with respect to both the average values and the dispersion of the values of the various body ratios and numerical characters listed on page 78. Data will be given also to show the changes that may occur in body ratios with increase in age and in length and differences that may exist between year classes with respect to numerical characters.

Tables 17 to 19 and 21 to 44 show the frequency distributions of the different body ratios and numerical characters for each for the four populations⁹⁾. In the body ratio distributions the size of the interval was determined arbitrarily in accordance with the range and dispersion of the character in question. In each table there are presented also the mean value¹⁰⁾ and the standard deviation of the character in each population. Because of the great diversity in the nature of the

⁹⁾ Certain discrepancies in the total number of individuals in the frequency tables for different characters should be explained. The O-group individuals of the Trout Lake cisco, because of their small size and poor condition (they were picked up along the beaches), gave unreliable data for certain characters and hence were omitted from the frequency tabulation. Occasionally the damaged condition of a specimen made the omission of a measurement necessary; for example, some fins were broken and could not be measured. Two Clear Lake ciscoes had distinctly abnormal adipose fins and were consequently omitted in the tabulation of L/AD for that lake. The counting of the branchiostegal rays was accidentally omitted for seven of the Trout Lake specimens.

¹⁰⁾ The mean values were computed from the individual specimens, not from the frequency groupings.

distributions, the probable error of the mean, although computed for each character, is not presented.

Tables 5 to 8 show the values for various body ratios according to age groups, and Tables 9 to 12 show the averages for the numerical characters according to year classes. Since all the specimens from Trout, Muskellunge, and Silver lakes were collected in the same year (1931) the division of the data for these lakes is the same whether it is made according to age or year class. Collections were taken from Clear Lake, however, in both 1931 and 1932. In combining the body ratio data for the two years' collections from Clear Lake the material for corresponding age groups were combined. For the numerical or fixed characters in the Clear Lake data, fish of the same year class were combined; that is, the data for each age group in the 1931 collection were combined with those of the next higher age group in the 1932 collection.

Tables 13 to 16 show the change with increase in length for those characters that show a change with increase in age. Separate tabulations of the changes of character values with respect to size and age are necessary, since the natures of the change with size and the change with age are not always the same. For example, it will be pointed out later that while relative head size tends to increase with increase in age, a division of the specimens into length groups independent of age shows no corresponding change of head size with length.

In the comparison of the four populations with respect to the various morphological characters considered here, attention will be called to the correspondence between the order of arrangement of the lakes with respect to the value of certain of the characters and their order of arrangement with respect to the rate of growth of their cisco populations. As was pointed out in an earlier section of this paper (page 74) the Trout Lake and the Clear Lake forms stand out definitely as the populations with the poorest and the best growth, respectively. The Muskellunge cisco appears to grow in length at the expense of depth and width with the result that this growth is superior to that of the Silver Lake cisco. On the other hand, the growth in weight of the Silver Lake cisco is superior to that of the Muskellunge Lake fish. The decision as to which of the two populations has the better growth depends largely on the point of view. In the following discussion it will be considered that if the Trout Lake cisco has the highest value for a character and the Clear Lake cisco the lowest (or the reverse),

while the Muskellunge Lake and Silver Lake forms show intermediate and similar values, then there is a correspondence between the order of arrangement of the lakes with respect to the rate of growth of the cisco and the value of the character under consideration.

In the discussion of each character specific reference will be made to the table that shows the frequency distributions of that character in the entire sample from each population. However, since all references concerning the change of characters with age (Tables 5 to 8), differences between year classes (Tables 9 to 12), and changes of characters with length (Tables 13 to 16) are based on the same tables, to avoid repetition, specific references will not be made to these tables.

Head in length (Table 17). The four populations are distinct from each other in the relative size of head, but in spite of the differences that exist there is a high percentage of overlap in the frequency distributions of L/H . The order with respect to the ratio L/H is the same as that with respect to growth rate. The slight tendency, noticeable in each population, for the head to become relatively larger as the individuals increase in age is in disagreement with the observations of Van Oosten (1929) who found that head size remains constant with increase in age in *L. artedi* of Lake Huron¹¹). If the change of L/H with increase in size, independent of age, is examined, it will be seen that on the whole the value of L/H shows little tendency to change consistently with increase in length. A possible explanation of the tendency for L/H to decrease with increase in age, but remain constant with increase in length, will be offered in the next section (page 100).

In the Clear Lake cisco the females have a slightly higher value of L/H than the males. This sex difference in head size is more apparent in the comparison of the samples of the same age than in the comparison of samples of the same length. The reason for the greater value of L/H in the females of the Clear Lake cisco will be brought out later (page 100).

Depth in length (Table 18). Here, again, with the possible exception

¹¹) It appears to be impossible to offer any generalization on the question of the differential growth of the head in coregonids. The observations of this investigation are in agreement with those of Lechler (1930) on *Coregonus fera* of the Mondsee. Freidenfelt (1934) showed that different forms of coregonids in the same lake may be unlike in the matter of differential growth of the head. According to Freidenfelt the relative head size decreases with increased body length in *Coregonus oxyrhynchus* on Wener See while in *C. maraena* in the same lake relative head size does not change with increase in body length.

of the Trout Lake and Silver Lake ciscoes, the four populations appear to be distinct from each other, although there is considerable overlap between the frequency distributions of L/D for any two populations. The order of arrangement of the average values shows no correspondence with growth rates. The Trout Lake fish, although the slowest growing, stand second to the Clear Lake cisco in relative depth of the body. In the Clear Lake cisco the average value of L/D is slightly greater in the males than in the females.

The examination of the data on the changes of L/D with increase in age and in length shows: (1) relative body depth changes only slightly with increase in length and in age in the Trout Lake and Silver Lake cisco populations; (2) L/D increases with size and age in the Muskellunge Lake cisco; (3) L/D decreases with size and age in the Clear Lake cisco; (4) in the Clear Lake cisco the females do not show consistently smaller values of L/D than males of the same size — hence the average difference between two sexes with respect to L/D depends on the greater abundance of large female fish in the sample.

The marked increase in relative depth with increase in length and age in the Clear Lake cisco and the decrease in relative depth with increase in length and age in the Muskellunge Lake cisco have an important bearing on the use of the relative depth of body as a systematic character. Certainly it is not valid to compare populations with respect to this character without knowledge of the manner of variation of depth with increase in size and age. Further, it is impossible to obtain a definitive value of L/D , characteristic of the population, in a stock where the character is subject to great change with continued growth. The value of such an average would be too much dependent on the length distribution of the sample used, and would vary not only according to the selection of the gear used in collecting the sample, but also from year to year according to the age and size composition of the population.

Width in length (Table 19). With the possible exception of the Trout Lake cisco and the Muskellunge Lake cisco the four populations are distinct from each other with respect to L/W . There is, however, a high degree of overlap between any two frequency distributions of the character. In the Clear Lake cisco the females show a lower average value of L/W than the males. A correspondence exists between the arrangement of the populations with respect to growth rate and the average value of L/W . The Trout Lake cisco, with the slowest

growth, has the relatively thinnest body while the fast-growing Clear Lake cisco has the relatively widest body. The Muskellunge Lake cisco and the Silver Lake cisco are intermediate with respect both to growth rate and the relative width of the body.

The changes of L/W with increase in age and in length are similar to those of L/D ; the ratio, L/W , changes slightly with age and length in the Trout Lake and Silver Lake ciscoes, increases with increased age and length in the Muskellunge Lake cisco, and decreases with increased age and length in the Clear Lake cisco. A further point of resemblance between L/W and L/D lies in the fact that the sex differences found in the average values of L/W in the Clear Lake cisco do not appear consistently in the comparison of males and females of the same length. The consideration of relative width, along with relative depth throws light on the typical body forms of the four populations. The Trout Lake cisco, which has the second deepest and the thinnest body tends to keep throughout life a rather thin but deep body form. The Muskellunge Lake cisco is much more terete, and becomes more slender with increase in length and age. In the Silver Lake cisco relative width increases somewhat with growth as does relative depth. On the whole, however, the change in general body form is not pronounced. It is the Clear Lake cisco that shows the most pronounced change of body form with increase in length and age. The great change that takes place in the appearance of the Clear Lake cisco as a result of the alteration of body proportions with growth is brought out by the comparison of the juvenile (I-group, in second summer) and adult specimens (Figure 4). At the top and middle of the plate the juvenile and adult individuals are photographed to the same scale. In order to illustrate better the differences between the two, a second reproduction of the juvenile fish, this time at such a scale that it appears to equal the adult in length, is presented at the bottom of the plate. This last illustration makes possible a direct comparison of the adult stature of the Clear Lake cisco with that which it might be expected to have if growth proceeded without change of body form. The comparison shows that while the young Clear Lake cisco possesses the slender body generally characteristic for the species, the differential growth along the vertical and lateral axes brings about the loss of this „herring“ form and leads to an exceptionally heavy adult stature.

The nature of the changes of form with growth in the four cisco

populations may be illustrated further by the equations that show the relationship between length and weight. These equations (Table 20 taken from Table 27 of Hile's (1936) study of the growth of the cisco) support the morphometric data in showing that: (1) the Muskellunge Lake cisco becomes more slender rapidly with increase in length; (2) the Trout Lake cisco becomes slender with increase in length, but at a lesser rate than the Muskellunge Lake cisco; (3) the Silver Lake cisco becomes relatively heavier with increase in length; (4) the Clear Lake cisco also becomes relatively heavier with increase in length, but at a greater rate than the Silver Lake cisco.

Adipose-to-caudal distance in length (Table 21). The Silver Lake cisco shows the smallest average value of L/AT , and the Clear Lake form the largest. The range of variation for the character is large. There is no correspondence between the arrangement of the four populations with respect to the average value of L/AT and with respect to growth rate. In none of the populations is there a consistent trend toward a change in the value of the ratio with increase in age.

Depth of caudal peduncle in length (Table 22). The values of the ratio, L/DCP , show close correspondence with the ratio, L/D , both as to the arrangement of the populations with respect to the character, and also as to the manner of change with growth (page 82). The use of L/DCP in systematic work is therefore obviously open to the same criticisms as the use of L/D .

Dorsal fin base and anal fin base in length (Tables 23 and 24). The Clear Lake cisco stands well apart in its relatively long dorsal fin base. The differences between the populations in the relative size of the anal fin base are smaller, although the Trout Lake and Clear Lake forms have distinctly the relatively longest anal fin base. Neither of the ratios, L/DB and L/AN , shows a consistent tendency to change in value with increase in age. The variations of the two ratios, L/DB and L/AN , appear to be independent of each other, that is, the possession of a high or low value of L/DB by a population or an age group does not mean that the same population or age group will possess a correspondingly high or low value of L/AN .

Length of adipose fin in length (Table 25). The four populations do not show great differences as to relative length of the adipose fin. The Trout Lake and Clear Lake ciscoes have the shortest adipose, and the Silver Lake cisco the longest. The range of variation of this character is so great that, unless very large numbers of specimens are used, it can have very little systematic value. In the Clear Lake cisco there appears a slight tendency for the adipose to become relatively longer with increase in age.

Pectoral-ventral distance in length (Table 26). The order of the populations with respect to the value of the ratio, L/PV , is the same as with the ratio, L/DB . Again the Clear Lake cisco shows a relatively greater length of this middle region of the body. The value of L/PV shows no consistent change with age, except that the Clear Lake I-group has a considerably higher value of the ratio than the succeeding age groups. The same was true of the ratio L/DB .

Diameter of eye in length (Table 27). The populations are distinct in the average relative size of the eye. In the fastest growing population (Clear Lake) the eye is relatively smallest, and in the slowest growing population (Trout Lake) it is largest. In Clear Lake the females have a greater average value of the ratio than the males. The range of variation of the character is so great that large samples must be used to obtain reliable average values. The variation in the relative size of the eye from one age group to another is irregular, and appears to depend to some extent upon the relative size of the head (see page 101).

Ventral-anal distance in pectoral-ventral distance (Table 28). The differences between the populations are, on the whole, small, although the Silver Lake form has a slightly higher average value for PV/AV than the other populations. There is no noticeable trend toward a change with age in the value of the ratio.

Snout in length of head (Table 29). The relatively shortest snout occurs in the Clear Lake population, the longest in the ciscoes from Silver Lake and Trout Lake. The values of H/S vary over a wide range and hence there is a high percentage of overlap between the frequency distributions of the different populations. The differences among the different age groups are considerable, but with the possible exception of the Trout Lake cisco where H/S tends to increase slightly with age, follow no trend. In spite of its great variability this character has been used widely in systematic studies of the subspecies of *artedi*.

Diameter of eye in length of head (Table 30). In the average value of the ratio, H/E , as of the ratio, L/E (Table 27), each of the populations stands a distinct from any of the other populations. The order in which the populations arrange themselves is, however, slightly different, Trout Lake and Muskellunge Lake having changed their relative positions. The eye of the Trout Lake cisco, when considered in relation to total length is the largest in any of the populations, but this situation apparently depends upon the fact that the Trout Lake form

possesses the relatively largest head (Table 17). The Muskellunge Lake cisco has the largest eye if size of eye is considered in relation to the length of the head. The head of the Muskellunge Lake cisco is, however, relatively smaller than that of the Trout Lake fish (Table 17). From the standpoint of growth the ratio, H/E , in a sense furnishes a better basis of description than the ratio, L/E . The head must be recognized as a semi-independent growth system. Consequently the relationships between the head and its parts are probably more significant than the relationships between the parts of the head and the entire body.

The range of variation of the ratio, H/E , is large in each of the populations.

In the Clear Lake cisco the I-group has an eye relatively larger than have the older groups. On the other hand the younger of the two age groups in the Muskellunge Lake collection has decidedly the smaller eye. In the Trout Lake and Silver Lake populations the ratio, H/E , shows no tendency to change in value as age increases. The tendency for the Clear Lake females to have smaller eyes than the males, because of its dependence on sex differences in the size of the head, is much less apparent in the comparison of the values of H/E in the two sexes than was the case with the ratio, L/E .

Length of maxillary in length of head (Table 31). There is correspondence between the order of the populations with respect to the value of the ratio, H/M , and their order with respect to growth rate. The fastest growing, Clear Lake form has by far the shortest maxillary, and the slowest growing, Trout Lake form the longest, while the Muskellunge Lake cisco and the Silver Lake cisco have maxillaries of about the same length and intermediate in size. The value of the ratio does not change with increase in age in any of the populations.

Diameter of eye in body depth (Table 32). The ratio D/E serves chiefly to bring in sharp relief the position of the Clear Lake cisco as a small-eyed, robust-bodied form. The four populations, with the possible exception of the Trout Lake and Muskellunge Lake stocks, are distinct with respect to this character. In the Trout Lake cisco and the Silver Lake cisco the changes of D/E with increase in age and with increase in length are irregular and without a definite trend. The ratio, D/E , decreases with increase in age and length in the Muskellunge Lake cisco and increases with increase in age and length in the Clear Lake cisco.

Length of pectoral fin in pectoral-ventral distance and length of ventral fin in ventral-anal distance (Tables 33 and 34). The relative length of the paired fins in the four populations shows a correspondence with the rate of growth. The slowest growing population (Trout Lake) has the relatively longest fins, and the fastest growing (Clear Lake) the shortest. The paired fins tend to be longer in the males than in the females, although this sexual dimorphism is not always evident in the younger age groups. With the exception of AV/V in the Silver Lake cisco it is not found in any of the I-group samples. The males have longer fins than the females in the small II-group samples from Clear Lake, Trout Lake and Silver Lake, but not in the II-group from Muskellunge Lake. As the individual becomes older and longer there is a slight tendency for the relative size of the fins to increase, especially in the males. This conclusion that the relative size of the paired fins increases with growth is precisely the reverse of Pritchard's (1931) findings on *L. artedi* of Lake Ontario. However, an apparent decrease in relative fin length with increase in body length might well result from the examination of data without respect to sex differences, since the shorter finned females are relatively more abundant in the higher age groups than in the lower. Although Pritchard recognized that the males of *L. artedi* have relatively longer fins than the females, his Table 8 showing the decrease of fin size with increase in length contains no division of data according to sex.

There is, furthermore, a tendency for the pectoral and ventral fins to vary together, that is, an age group, population, or sex that shows a high or a low value for ratio, PV/P, may be expected to show a corresponding high or low value for the ratio, AV/V.

The relative lengths of the paired fins have been used as an important character in the separation of the subspecies of *L. artedi*. However, Koelz (1931) in the preparation of a key to the subspecies of *artedi* made no mention of sex differences in the size of the paired fins.

Dorsal base in height of dorsal fin (Table 35). Here, again, the fastest growing population has the relatively shortest fins and the slowest growing the longest. In the Clear Lake samples the ratio DH/DB decreases sharply from the I-group to the II-group, but remains fairly constant thereafter. In the other populations the value does not change with age.

Gillrakers on the first branchial arch (Table 36). Although there is a high percentage of overlap between the distributions of the number

of gillrakers (R) on the first branchial arch, the Clear Lake cisco may be considered as distinguished from the other three populations by the possession of the highest average number of gillrakers. The gillrakers have been considered by many interested in the systematics of the coregonids to be a highly reliable diagnostic character. An argument for a high degree of constancy in this character appears in the comparison of the 1931 and 1932 Clear Lake collections. The 61 specimens of the 1931 Clear Lake collection and the 95 specimens in the 1932 collection from the same lake each gave an average value of 48.4 rakers. Such close agreement is striking, particularly in view of the indicated dispersion and range of variation. It must be remembered, however, that the two years' collections of the Clear Lake cisco were composed largely of individuals of the same year classes. With the single possible exception of the III-group and the V-group (1928 and 1926 year classes) of the Silver Lake cisco the differences in raker number between year classes¹²⁾ of the same population can not be considered significant (see page 118).

Scales in the lateral line (Table 37). The range of variation in the number of lateral line scales (Sc) is large in each population. The Trout Lake cisco has, on the average, from 5.5 to 7.0 fewer scales in the lateral line than the remaining three forms. Because of the great range of variability this character is probably of little systematic value. The differences between year classes of the same population for this exceptionally variable character are not large.

Dorsal scale rows (Table 38). The Trout Lake cisco has the smallest number of dorsal scale rows (RD), the Clear Lake cisco the largest. The Muskellunge Lake and the Silver Lake forms are practically identical both as to the average number of dorsal scale rows and as to the nature of their frequency distribution. Within a population the different year classes show remarkably uniform values for the average number of dorsal scale rows.

Peduncle scale rows (Table 39). With reference to this character (RC) the populations differ both as to the average value and as to the type of dispersion. In the Muskellunge Lake samples not one individual varies from the characteristic number of 22 peduncle scale rows. In the Trout Lake cisco a mode occurs at 21, but more than half the individuals have either 22 or 20 scale rows, while an insigni-

¹²⁾ For all numerical characters comparisons are made on the basis of year classes rather than age groups. See page 80.

ficant few have either 23 or 19. In the Silver Lake collection more than half of the individuals have 21 peduncle scale rows, while all but one of the remaining individuals have either 22 or 23 rows. The Clear Lake cisco stands apart in the possession of the greatest number of peduncle scale rows, practically all fish having either 24 or 25 rows. Different year classes of the same population show insignificant differences in the number of peduncle scale rows.

It will be noticed that with respect to both the number of dorsal scale rows, and the number of peduncular scale rows, the four populations arrange themselves in the order of their growth rates. Since it is well known¹³⁾ that after the laying down of the individual foci the number of scales can be considered a fixed character, it can hardly be assumed that this arrangement is the direct result of differences in growth rate after the time of scale formation. It is possible, however, that the same conditions that determine the general growth histories of the four populations may serve to modify their various rates of development up to and during the time of scale formation in such a way as to produce the arrangement observed above in the average values for the number of dorsal and peduncular scale rows.

Branchiostegal rays (Table 40). The Clear Lake cisco has the highest average number of branchiostegal rays (BR) and the Muskellunge Lake cisco the lowest average number. In Muskellunge Lake most of the fish have eight branchiostegal rays while in Clear Lake most of the specimens have nine rays. In Silver Lake and Trout Lake the modes are not so sharp. In spite of the overlap that exists, some of the differences between the populations may be considered significant. The differences in the number of branchiostegal rays in different year classes of the same population are small and without significance.

Rays in the dorsal (DR), anal (AR), pectoral (PR), and ventral fins (VR) (Tables 41 to 44). On the whole the differences between the populations in the number of fin rays are not large. The stocks with the smallest average number of rays are: dorsal rays — Clear Lake; anal rays — Trout Lake; pectoral rays — Trout Lake; and ventral rays — Muskellunge Lake. The stocks with the greatest average number of fin rays are: dorsal rays — Muskellunge Lake; anal rays —

¹³⁾ Van Oosten (1929) showed that the number of scales in the horizontal scale rows of *L. artedi* in Lake Huron may be considered constant for a year class. The same conclusion probably applies to the number of scales in vertical scale rows.

Silver Lake; pectoral rays — Silver Lake; and ventral rays — Silver Lake. When the number of specimens is large the various year classes of the same population show only slight differences in fin ray number.

Table 45 provides a summary of the differences among the populations with respect to each of the characters considered in the preceding pages. The numbers listed in the table are in the nature of „index“ numbers. To illustrate the method of their derivation, consider the ratio, L/H . The Trout Lake cisco has the relatively largest head, and hence the lowest average value of L/H . This value of L/H in the Trout Lake cisco is listed in Table 45 as 1.00. The value of L/H in the Muskellunge Lake cisco is 1.09 times that of the Trout Lake cisco; in the Silver Lake cisco the value of L/H is 1.14 times that of Trout Lake; and finally, in the Clear Lake cisco the average for L/H is 1.17 times that found in the Trout Lake form. The numbers listed for the remaining characters have the same significance; the lowest average value of a character is given an index number of 1.00, and the higher average values are assigned index numbers according to their deviation from the lowest average. A further idea of the general appearance of the four populations may be had from the illustrations of typical specimens (Figures 3 and 4).

From the data of the preceding pages the following conclusions may be drawn:

(1) With respect to most morphometric characters, particularly the body ratios, these four inland lake cisco stocks show very wide ranges of variation. Because of these wide ranges of variation reliable averages can be obtained only from large numbers of specimens. Such highly variable characters are obviously of limited systematic value.

(2) In spite of the high percentage of overlap between the frequency distributions of the morphometric characters in the different lakes, the four populations show significant differences with respect to most of the body ratios and numerical characters. Resemblances between two stocks with respect to any one character are offset by dissimilarities with respect to other characters. If the data are considered as a whole each of the four populations must be considered as distinct from any one of the others.

(3) In all four populations the male specimens (except in certain of the younger age groups) have longer paired fins than the females. Other sex differences are confined to the Clear Lake cisco where the

female specimens have the higher average values for L/H , L/E , and H/E , and the lower average values for L/D and L/W .

(4) Certain body ratios (L/D , L/DCP , L/W , D/E , PV/P , AV/V) show distinct tendencies to change with an increase in the age and size of the fish. The direction of change may not be the same in different



Figure 3. — Typical specimens of the cisco:
(a) from Trout Lake (length, 122 millimeters); (b) from Muskellunge Lake
length, 152 millimeters); (c) from Silver Lake (length, 171 millimeters).

populations. For example, relative body depth increases with age and length in the Clear Lake cisco but decreases with growth in the Muskellunge Lake cisco. It is very difficult to compare populations with respect to characters that change with growth without a thorough

knowledge of the extent and rate of such change. Nor does a single average value describe a population adequately with respect to such characters, particularly if the change in the value of the character with growth is large.

The ratio, L/H , shows a tendency to decrease with age, but a division of the specimens into length groups irrespective of age fails to reveal a corresponding tendency for L/H to decrease with length. (See page 100.)

(5) The average values of certain characters (L/H , L/W , L/E , H/M , PV/P , AV/V , DH/DB) show a striking correspondence with the growth rates of the different stocks. The slowest growing population (Trout Lake) has relatively the longest head and maxillary, the largest eye, the least body width, and the longest pectoral, ventral, and dorsal fins, while the fastest growing population (Clear Lake) has relatively the shortest head and maxillary, the smallest eye, the widest body, and the shortest pectoral, ventral, and dorsal fins. The Muskellunge Lake cisco and the Silver Lake cisco are intermediate to the Trout Lake cisco and the Clear Lake cisco, both as to growth rate and as to the above named morphological characters. The question of the significance of these apparent relationships between growth rate and morphological characters will be considered in greater detail in the next section.

The morphometric data of this section are further of interest as they relate to the currently accepted definitions of the subspecies *clarensis* and *clemensi*. As was pointed out in the introduction (page 59), the ciscoes of Muskellunge, Silver, and Clear lakes were referred by Koelz (1931) to the subspecies *clarensis* while the Trout Lake cisco was classed with the subspecies *clemensi*. The type locality of *clarensis* is Clear Lake, while that of *clemensi* is Lake Nipigon, Ontario. According to Koelz both subspecies are members of the group with „Gillrakers on the first branchial arch usually more than 45“, and „Body slender; L/D usually more than 4.“ Koelz (1931) separates his subspecies *clemensi* and *clarensis*, on the following characters:

<i>clemensi</i>	<i>clarensis</i>
PV/P usually less than 1.9	PV/P usually more than 1.8 in specimens over 200 millimeters long.
Gillrakers usually 46—49.	Gillrakers usually 46—51 but frequently fewer.
H/M 2.7—2.9.	H/M usually 2.9—3.1.
H/S 3.7—4.	H/S usually 3.9—4.2.
Lateral line scales usually 71—76.	

Koelz' key offers no information as to the number of lateral line scales in *clarensis*.

It should be mentioned that Koelz did not include the opercular membrane in his measurement of head length. For that reason his values for ratios that involve head length would be expected to differ

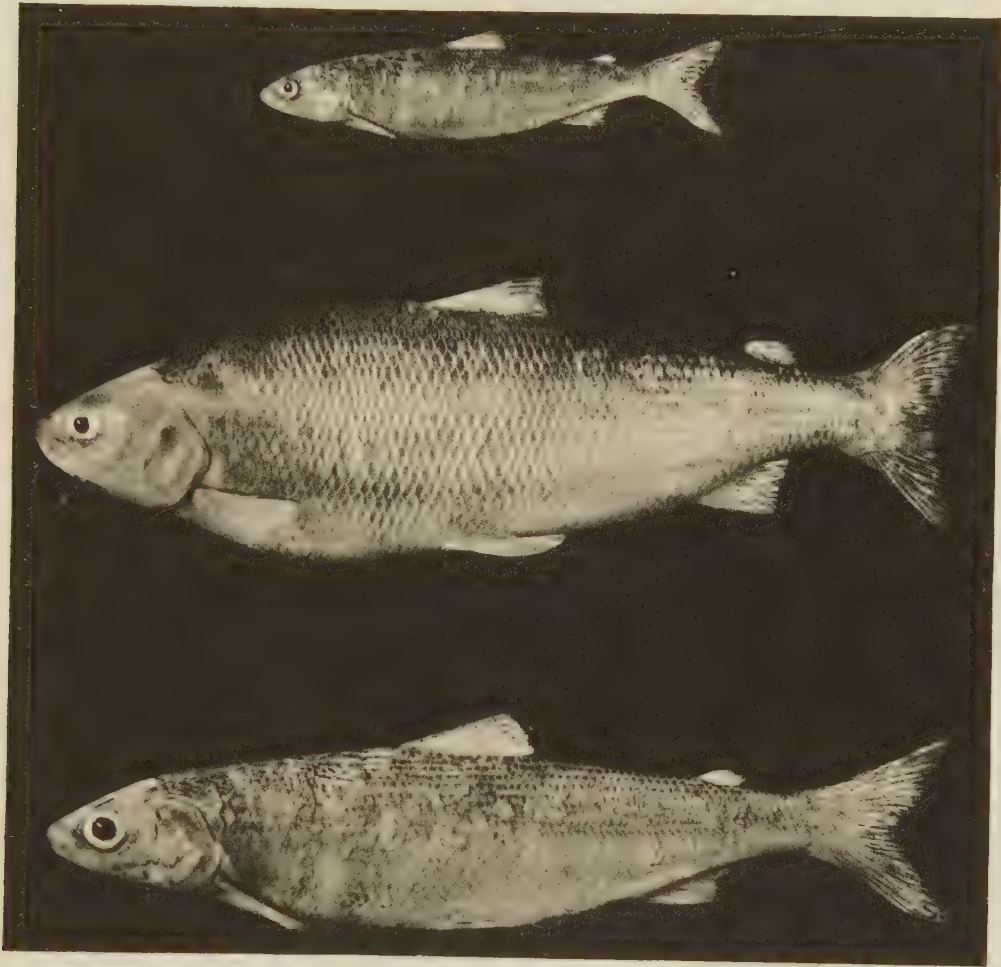


Figure 4. — Typical specimens of the Clear Lake cisco:
(a) juvenile (length, 167 millimeters); (b) adult (length, 326 millimeters);
(c) the juvenile, a, to a larger scale.

from those recorded in this study. The disagreement should be confined, however, to the actual values of the ratio and should not alter the conclusions to be drawn from a comparison of the two subspecies.

In the text of his 1931 paper Koelz made the following observations concerning the populations from Trout, Muskellunge, and Silver lakes:

Trout Lake: „They appear to be very similar to typical *clemensi*.“

Muskellunge Lake: „The race is much like typical *clarensis*.“

Silver Lake: „The form is much like *clarensis*, but seems to approach *sisco* in the matter of head length and in the number of gillrakers.“

Koelz examined 16 specimens from Trout Lake, 42 from Muskellunge Lake, 23 from Silver Lake, and 46 (type and 45 paratypes) from Clear Lake. Thirty-nine of the paratypes in his collection from Clear Lake ranged in length from 135 to 200 mm. These fish were almost certainly members of the I-group. The remaining six paratypes ranged in length from 227 to 306 mm.

The data presented by Koelz, particularly in view of the great variability of the cisco, furnish a very indefinite basis for the separation of *clarensis* and *clemensi*. It is only with respect to the relative length of the maxillaries that a definite separation was indicated between the two subspecies. Nevertheless the data of the present investigation show that the populations from Muskellunge Lake and Silver Lake resemble the Trout Lake cisco (*clemensi*) more closely as to the length of maxillary than they resemble the *clarensis* type form from Clear Lake (Table 31). It should be noted further that no reference is made by Koelz to sex differences in the relative length of the pectoral fin. However, the present study has proved that sex differences in fin size do exist¹⁴).

With reference to the relationships showed by the four populations

¹⁴) Altogether aside from the question of the validity of either of the two subspecies, it should be mentioned that Koelz was particularly unfortunate in his selection of Clear Lake as the type locality for *clarensis*. Unquestionably he wished to include under *clarensis* a great number of populations of small, slender bodied, short snouted ciscoes that are characteristic of many of our more northerly lakes. The Clear Lake cisco is by no means such a small, slender bodied form. The examination of Koelz' data on the length distribution of his Clear Lake specimens shows clearly the source of his error. Forty of the fish he examined had a length of 200 millimeters or less. At this size the Clear Lake cisco is indeed the slender fish that *clarensis* was intended to represent (See Figure 4). It is only with further growth that this juvenile appearance is lost, and of the larger, heavy-bodied fish Koelz had no adequate representation. That the few larger fish that he did examine gave Koelz no inkling as to the true adult stature of the Clear Lake cisco is apparent from the fact that he selected for his type specimen a juvenile individual only 178 millimeters long. If the use of the name *clarensis* is to be continued at all it must obviously be confined to the Clear Lake form.

of this investigation, it may be repeated that each population is absolutely distinct from the others. This conclusion is supported not only by the morphometric data but also by the general appearance of typical specimens from each lake (See Figures 3 and 4). The Muskellunge Lake and Silver Lake ciscoes in general resemble the Trout Lake *clemensi* population more than they do the Clear Lake *clarensis* type, but the differences that exist among all these four populations are on the whole greater than those that have been employed for the separation of the subspecies *clemensi* and *clarensis*. As will be brought out in a more general consideration of the systematic problems of the species *L. artedi* (page 118), it is nevertheless highly questionable whether the differences between these four populations necessitate or even make valid their separation into different systematic groups.

Variations within a population.

Growth rate and body form.

In the preceding section attention was called to the fact that when the cisco populations from Trout Lake, Muskellunge Lake, Silver Lake, and Clear Lake are arranged in the order of their growth rates, they show the same arrangement that they show with respect to the average values of certain body ratios (L/H , L/W , L/E , H/M , PV/P , AV/V , and DH/DB). The arrangement was such that more rapid growth was associated with a relatively shorter head, smaller eye, shorter maxillary, wider body, and shorter fins. The correspondence of the arrangements suggests that the differences between the populations with respect to these body ratios may depend, in part at least, on differences in the growth rates of the four stocks. If this correspondence between morphometric characters and growth rate is to be considered causal in the sense that the observed arrangements of the character values have resulted from differences in the growth rates of the four stocks, and hence from factors that produced these differences in growth rates, it is to be expected that the analysis of variation of these characters within a single population may show a dependence of individual ratio values on individual growth rate. Such an analysis was made for each of the ratios that showed a correspondence with growth rate. The ratio L/H will be considered first as an example of the method of procedure.

Tables 46 to 49 show for each population the values of the ratio, L/H , arranged according to age and length, that is, according to the

rate of growth in length¹⁵). Since this procedure necessarily involves a breaking of the sample into rather small subdivisions, some irregularities in the results are to be expected. Nevertheless, in spite of the exceptions that occur, the data indicate rather clearly that the relative length of the head does show a dependence on the rate of growth, detectable within a population. The smaller fish within an age group and the older fish within a size group, that is, the slower growing fish, tend to have the relatively larger heads. Further, a wide range of variation in individual growth is accompanied by a correspondingly great range of variation in the relative size of the head. This fact can be seen by a comparison of the variation of the ratio L/H in the different age groups of the Clear Lake cisco with that of the same ratio in the other three populations.

Since it is difficult from mere direct examination of the tables to determine how seriously the exceptions, resulting from the division of the samples into such small groups, may operate against the general thesis that within a population relative head length depends on growth rate, it is deemed advisable to offer a more definite measure of the strength of the tendency for individual relative head length to be correlated with individual growth rate. Such a measure can be obtained through the determination of the total amount of change in the ratio,

¹⁵) In analyses of the type found in Tables 46 to 49 it is important that the samples for a single lake be taken at approximately the same time in the growing season. Otherwise individuals of the same age might show differences in length that depend on the time of capture within the growing season rather than on individual differences in growth rate. The dates of collection of the Trout Lake material (Table 46) were July 11 to 15 and July 22, 1931; of the Muskellunge Lake specimens (Table 47) July 14 and July 31, 1931; of the Clear Lake specimens (Table 49) July 12 to 19, 1932; and of the Silver Lake material July 17 and August 22, 1931. Since the Silver Lake collections were taken more than a month apart it was not considered advisable to combine them for the study of the relationship of individual growth rate and individual size of head. Hence, in Table 48 the data for all ages (129 fish) above the I-group are based on fish captured July 17, 1931, while the I-group fish were all taken on August 22, 1931. The inclusion in Table 48 of these I-group individuals, whose capture was made possible by a change of gear after July 17, is quite justifiable since there are no comparisons of I-group fish with older fish of the same length. The 61 preserved specimens taken in Clear Lake in 1931 likewise were not employed since they were captured over two widely separated periods, the first in late July and the second in early September, and each of the single collections is too small to be of value for the study of the effect of individual growth rate on individual head size.

L/H, first with increase in size within an age group and second with increase in age within a size group. The following examples will illustrate the procedure.

It may be seen in Table 48 that the V-group Silver Lake ciscoes of the length interval, 175—179, millimeters have a value for L/H of 4.33. This value is 0.21 greater than the L/H value of 4.12 in the 170—174 millimeter interval of the same age group. The 170—174 millimeter interval is represented by three specimens, and the 175—179 millimeter interval by eight. If each specimen of the former interval were compared with each specimen of the latter interval, a total of 24 comparisons would be possible. Since, on the average, a change from the lower to the higher length interval is associated with an increase of 0.21 in the value of L/H, the total change between the two intervals, based on all possible comparisons, is 24×0.21 or 5.04. Similarly, the data for the 175—179 millimeter and the 180—184 millimeter interval show a total number of comparisons, $8 \times 13 = 104$, each one of which is associated with an average change of -0.03 in the value of L/H. The total change between these two intervals may be taken as 104×-0.03 or -3.12 . A continuation of the same procedure shows that the total change from the 180—184 millimeter interval to the 185—189 millimeter interval is 15.21; the change from the 185—189 millimeter interval to the 190—194 millimeter interval is 5.04; and finally the change from the 190—194 millimeter interval to the 195—199 millimeter interval is 0.14. The total value of the positive changes is 25.43, and this value may be taken to represent the tendency for the value of L/H to increase with increased length of the fish in the V-group of the Silver Lake cisco. The total negative change of -3.12 represents the tendency for the value of L/H to decrease with increased length of the fish in the same age group. Thus it may be seen that in the V-group of the Silver Lake cisco the tendency for the relative size of the head to be smaller in the large fish is almost eight times as great as the reverse tendency for the larger fish to have relatively larger heads, and that the single exception (from the 175—179 to the 180—184 millimeter group) is of little importance. If the corresponding data for all age groups of the Silver Lake cisco are combined there is obtained a total positive change of 64.67 as against a total negative change of -10.31 . From these quantities it may be concluded that in the Silver Lake cisco population as a whole the tendency for the larger fish within an age group to

have relatively smaller heads than the smaller fish of the same age group is more than six times as great as the tendency for the larger fish of an age group to have relatively larger heads than the smaller individuals of the group.

A similar method may be used to measure the relationship between the value of L/H and the age of individuals in the same length group. As an example consider the 175—179 millimeter interval of the Silver Lake cisco (Table 48). Between the II-group and III-group fish of this length interval there are six possible comparisons. Each comparison is associated with a change of -0.36 in the value of L/H (from 4.73 in the II-group to 4.37 in the III-group). The total change from the II-group to the III-group is 6×-0.36 or -2.16 . Similarly, the change from the III-group to the IV-group is 78×-0.05 or -3.90 ; and the change from the IV-group to the V-group is 104×0.01 or 1.04 . The total negative change in the 175—179 millimeter interval is -6.06 and the total positive change is 1.04 . Thus it may be seen that within this length interval the tendency for the older fish to have relatively longer heads than the younger fish of the same interval is almost six times as great as the tendency for the younger fish of the interval to have relatively larger heads than the older fish. If the corresponding data for all length intervals are combined, the total negative change for the entire Silver Lake population is -63.26 while the total positive change is $+1.34$. From these quantities it may be concluded that in the entire Silver Lake cisco population the tendency for the older fish of a length interval to have relatively longer heads than the younger fish of the same interval is about 47 times as great as the reverse tendency for the younger fish of a length group to have relatively longer heads than the older fish of the same group.

The data from all four populations (Tables 46 to 49) were subjected to analyses of the type just illustrated. The results of these analyses appear in Table 50. To facilitate a direct comparison of the data for the different lakes all ratios have been reduced to a common basis. For example, in the study of the relationship between length and relative head length in the Silver Lake cisco the value of the ratio of the total positive changes of 64.67 and the total negative changes of -10.31 can be expressed by the ratio, $1.000:0.159$. Similarly, in the study of the relationship of age to relative size of head of fish in the same length group in Silver Lake the value of the ratio of the total negative changes of -63.26 to the total positive changes of

1.34 may be expressed as 1.000 : 0.021. (The ratios are based on absolute values, that is, without reference to plus and minus signs.) These modified ratios as they appear in Table 50 are all directly comparable¹⁶⁾

The examination of Table 50 shows that, on the whole, the exceptions to the general trends of Tables 46 to 49 are of minor importance as they affect the general conclusion that individual relative head length is correlated with individual growth rate. In the Muskellunge Lake cisco the tendency for the more rapidly growing fish of an age group to have the relatively larger heads is almost two fifths as great as the tendency for them to have the relatively smaller heads, but in none of the other lakes are the exceptions so important. The data of Table 50 show further that the correlation between age and relative head length in fish of the same length group is closer than the correlation between body length and relative head length in fish of the same age.

Although the data of Tables 46 to 49 show clearly that growth rate and relative size of the head are closely correlated, it is not valid to assume that the observed differences as to relative size of the head among the four populations are entirely dependent on differences in the growth rate of these populations. For example, the comparison of the relative size of the head in the III-groups of Muskellunge Lake and Silver Lake (Tables 47 and 48) shows that Muskellunge Lake ciscoes consistently have larger heads than Silver Lake ciscoes of the same length and the same age. Thus it may be seen that the Muskellunge Lake cisco and the Silver Lake cisco show differences in the relative size of the head that do not depend on differences in growth rate, but are either genetic or dependent on factors other than those that determine the growth rates of the two populations. Nevertheless the dependence of relative head size on growth rate as demonstrated in the preceding pages is sufficiently close to show that great caution should be used in the employment of relative head size as a diagnostic character in systematic studies of the cisco, particularly when these systematic studies may involve the comparison of popu-

¹⁶⁾ From the mathematical standpoint no high degree of refinement is claimed for this method of demonstrating a dependence of individual values of body ratios on individual growth rate. While the method may lack precision in the actual evaluation of the strength of such dependence, it is a quite valid and reliable means of demonstrating that the individual values of certain body ratios do depend on individual growth rate.

lations with greatly different rates of growth. It must be remembered further that the parts of the body of a fish must be in equilibrium. The presence of an unusually large or an unusually small head can be expected to bring about certain adjustments that may affect the values of other diagnostic characters.

The data of this investigation as they pertain to the dependence of individual relative head size on individual growth rate are in disagreement with the observations of Lechler (1930) on the Reinanke, *Coregonus fera* of Mondsee. Lechler found that in the *C. fera* the relative size of the head increases with increase in age (this is true also of the cisco populations of this study), but his examination of the variation of relative head size within a single age group showed that there is no difference with respect to this character between the larger and the smaller individuals of the same age. He concluded therefore that relative head size is dependent on age and not on length. In the present study of the cisco, relative head length has been found to depend on both age and length, that is, on growth rate.

The dependence of individual relative head length on individual growth rate offers an explanation of the general tendency for older age groups to have relatively larger heads. In the study of the growth of these cisco populations (Hile, 1936) evidence was presented that suggested that there might exist within a population a differential mortality based on rate of growth. If the rapidly growing individuals tend to be short lived, then the relative size of the head should be greater in the older age groups. Such a tendency for relative head size to decrease with age has been showed to exist in each of the four cisco populations (page 81). However, a division of the samples on the basis of size alone brings about such a mingling of slow growing and fast growing fish that there is no corresponding tendency for relative head length to increase with increase in size.

A second interesting consequence of the dependence of head size upon rate of growth appears in the Clear Lake collection in the comparison of the values of the ratio, L/H , for corresponding ages of the two sexes (Table 8). In the other three populations the two sexes show no difference as to growth in length, but in Clear Lake the female grows at a slightly more rapid rate than does the male. In a corresponding manner the females show rather consistently a higher value for the ratio, L/H , than do males of the same age. The average value of L/H for the 78 females in the entire collection is 4.53, while the value

of the ratio for the 78 males is 4.45. However, a comparison of the values of the ratio for males and females of equal growth rates was found to show no differences between the sexes. Twenty-four males gave a value of 4.47 for L/H as compared to a value of 4.46 for twenty-four females of the same size and the same age. This difference between the sexes in the relative size of the head might well be called „indirect“ sexual dimorphism. It originates not from an innate tendency for the females to form small heads, but rather from the tendency for the females to grow at a more rapid rate than do the males.

A further interesting consequence of the more rapid growth of the females appears in the comparison of eye size in the two sexes in the Clear Lake collections (Tables 8, 27, and 30). With respect to the ratio, H/E , there is but little indication of the existence of a difference between the sexes. The females show an average value of 4.75 for the ratio, and the males a value of 4.71. Thus the eye in the male is less than one per cent larger than the eye in the female. However, if eye size is compared on the basis of the ratio, L/E , the females appear to have a definitely smaller eye. The average value for the females is 21.52 and for the males, 20.86. Here the eye size of the male appears to be more than three per cent larger than that of the female. This sex difference in the value of the ratio, L/E , finds its origin largely in the fact that the more rapidly growing females develop relatively smaller heads than do the males. Similarly, the relative sizes of the maxillary and the snout show no sexual dimorphism in the Clear Lake cisco when expressed in terms of head length but would appear to be greater in the males if they were expressed in terms of total length. Pritchard (1931), referring to data published by him in an earlier paper (1928), stated that in ciscoes (*Leucichthys* spp.) in Lake Ontario the males have „slightly longer“ heads, than the females and „with them the head measurements, eye, snout, and maxillary“. It is possible that these differences that Pritchard noted result from a sex difference in the rate of growth.

Analyses similar to the one made to show the relative strength of the „expected“ tendency for rapid growth to be correlated with relatively short heads and the reverse tendency (exceptions) for rapid growth to be correlated with relatively large heads, were conducted also to show the relationship between individual growth rate and individual values of the ratios, L/E , H/M , L/W , PV/P , AV/V and DH/DB . The results of these analyses appear in Table 51. In order that the data

for all characters may be combined conveniently into a single table the quantity, 1.000, which represents the expected tendencies, has been omitted for each character. The ratios of this table are identical in significance with the corresponding ratios of Table 50. The comparisons between the II-group and the III-group of the Muskellunge Lake cisco although included in Table 50 for the sake of completeness are omitted from Table 51. The examination of Table 47 shows that this comparison is based on too few specimens to give reliable results.

The data of Table 51 show first that in all four populations the more rapidly growing fish of an age group tend to have relatively smaller eyes (antero-posterior diameter in relation to total body length) than the slowly growing fish of the same age group. This situation probably results in part from the tendency for the longer fish of an age group to have relatively smaller heads. The eye as a structural unit of the head would thus tend to be relatively smaller in comparison to total body length in these longer fish of the age group. The conclusion that individual relative eye size is correlated with individual growth rate is supported further by the fact that in the Trout, Silver, and Clear Lake ciscoes the more slowly growing fish of a length group show a distinct tendency to have relatively larger eyes than the younger fish of the same group.

Length of maxillary also appears to be closely correlated with growth rate in the Trout Lake cisco. In this population the more rapidly growing fish of an age group show a strong tendency to have relatively shorter maxillaries than the shorter fish of the same age groups. Further, the more rapidly growing fish of a length group also have the relatively shorter maxillaries. The correlation between relative size of the maxillary and growth rate is much weaker in the Muskellunge and Clear Lake ciscoes than in the Trout Lake cisco, while in the Silver Lake cisco individual relative length of the maxillary appears to be largely independent of individual growth rate. In Silver Lake the comparison of fish of the same length but of different ages shows that the exceptions are only about three fifths as great as the expected changes, while the comparison of fish of the same age but of different length shows the exceptions are 1.24 times as great as the expected tendency.

Since the populations with more rapid growth showed relatively greater width of body than the populations with slower growth it might be expected that the longer fish of an age group within a single

population would have relatively wider bodies than the smaller fish of the same age groups, and that the older fish of a length group would have relatively narrower or thinner bodies than younger fish of the same length. From the examination of Table 51, it is apparent that the data on relative body width fail almost completely to fulfill these expectations. In the Clear Lake cisco, it is true, the more rapidly growing fish of an age group tend to be relatively wider than the more slowly growing fish of the same age group but in Muskellunge Lake there is an overwhelming tendency for the more rapidly growing fish of an age group to be thinner than the more slowly growing ones, while in the Trout Lake cisco and the Silver Lake cisco the variation of relative body width within an age group appears to be independent of variation in body length. The data show further that in the Trout Lake, Silver Lake, and Clear Lake ciscoes the older fish of a length group tend to be relatively wider than the younger ones, not thinner as might have been expected, if L/W were dependent on growth rate. It may be concluded therefore that in general no correlation between relative body width and growth rate exists within a single population.

In general the relative lengths of the paired fins as based on the ratios, PV/P and AV/V , show a fairly close correlation with growth rate; that is, more rapid growth of body is correlated with relatively shorter paired fins. In the analysis of the variation of these two characters, the reduction, through the separation of the sexes, in the number of individuals in each group studied might be expected to lead to a greater number of irregularities. In some cases the argument for the dependence of individual relative length of the paired fins on individual growth rate is fairly weak. In the Silver Lake females, for example, the comparison of fish of the same age but of different length shows no correlation between growth rate and relative length of the ventral fins, while in the males of the same population the comparison of fish of the same length but of different age shows only a slight correlation between growth rate and the relative length of the pectoral fins. Most of the examples, however, indicate a fairly close relationship between growth rate and relative length of the pectoral and ventral fins.

The relative length of the dorsal fin, as based on the ratio DH/DB , as well as the relative length of the paired fins tends to be less in rapidly growing fish than in individuals with slow growth. In both the Silver Lake and Clear Lake populations, however, the tendency for the more

slowly growing fish of a length group to have the relatively longer dorsal fins is not very pronounced.

The data of the preceding pages show that the differences among the cisco populations of Trout, Muskellunge, Silver, and Clear lakes with respect to the average values of certain body ratios (L/H , L/E , H/M , PV/P , AV/V , DH/DB) may be explained in part as the result of differences in their growth rates. Although L/W , on the basis of the averages for complete samples, showed an apparent correlation with growth rate (page 82) the analysis of this section failed to reveal any dependence of relative body width on growth rate within a single population. It is quite possible that yet other ratios not employed in this morphometric study may show a similar dependence on growth rate. On the basis of these data it would appear reasonable to explain much of the variability of the body ratios of coregonids as observed by many investigators, both in the same and in different populations, as the result of the dependence of individual values of certain ratios on individual rate of growth. It should be pointed out further that body ratios whose values vary with variations in growth rate must be considered of limited value as systematic characters.

Attention should be called particularly to the fact that the practice, common among systematists, of comparing body ratios only in fish of the same length offers no assurance that the samples are really comparable, for two fish or groups of fish of the same size may have entirely different growth rates, and may consequently show differences in body ratios that depend only on these differences in growth rate, and hence are of no systematic significance. It would appear, therefore, that a knowledge of growth rates forms an indispensable part of the data for any systematic study of the coregonids. Whether two populations with widely different growth rates can be compared at all with respect to characters that show a dependence on growth rate is questionable.

Morphological differences between year classes.

If the cisco is to be considered a highly plastic form, and one readily modified according to varying environmental conditions, different year classes might be expected, at least exceptionally, to show basic morphological differences that depend upon differences in environmental conditions at the time of hatching and early development. Ordinarily the nature of the environment furnished by a lake does

not vary greatly from one year to another. Exceptional seasons, however, occur occasionally.

The collections of the present investigation provide one excellent example of two year classes which, though separated by only one year in age, show morphological differences of considerable magnitude. These differences are sufficiently pronounced to affect the entire appearance of the individuals, with the result that most of them can be assigned readily by sight to the one group or the other. The groups in question are the 1928 and 1929 year classes of the Muskellunge Lake cisco. They appeared in the material of the present investigation as the III-group and II-group of the 1931 collection, and as the IV-group and the III-group of the 1932 collection¹⁷). A comparison of the general appearance of the head in the two year classes may be made from the illustrations of typical specimens from each group in Figure 5. The most striking point of difference is the relatively larger eye in the 1928 year class. In fresh specimens it is apparent, further, that the 1928 year class individuals are more highly pigmented in the dorsal region. In the discussion to follow still other differences between these two groups will be mentioned.

In the study of the morphometric differences between the 1928 and 1929 year classes attention will be given first to the data of the 1931 collection. In this year's collection the 1928 year class was present as the III-group, while the 1929 year class was represented by the II-group. No other year classes were present in the 1931 Muskellunge Lake collection.

Table 52 shows the values, according to year-class and length of fish, of seven body ratios for which the 1928 and 1929 year classes showed statistically significant differences in the 1931 Muskellunge Lake cisco collection¹⁸). The mere fact that these differences are significant from the mathematical standpoint cannot, however, be taken as proof that the two year classes exhibit fundamental and permanent differences with respect to all these seven characters. The

¹⁷) The 1932 collections from Muskellunge Lake were made primarily for the investigation of the morphological differences between the 1928 and 1929 year classes, and consequently data from this year's (1932) collection were not included in the preceding sections. (See page 76.)

¹⁸) The two year classes as represented in 1931 also showed significant differences with respect to the ratio, D/E, but this ratio is not included in this analysis since the ratios, L/E and L/D, of which D/E may be considered a combination, are treated thoroughly.

differences might depend, for example, on differences in the growth rates of the two year classes; or, again, they might represent different stages in a natural change of body form with increase in length.

It can be demonstrated at once that the growth rates of the two year classes do not account for the structural differences between them indicated in Table 52. The growth histories of the two groups as based on the 110 specimens used in the morphometric study appear in Table 53. Although the differences in growth rate are not large, the 1928 year class appears to have grown at a slightly higher rate than the 1929 year class. It would hardly be expected that such small differences in growth rate would produce any extensive structural differences. However, if any such differences were to exist the slower growing 1929 year class would, in accordance with the conclusions reached in the preceding section, be expected to have the longer head, and the larger eye. The data of Table 52 show that precisely the reverse is true. It is the 1928 year class, not the 1929 year class, that has the longer head and the larger eye.

Since it was demonstrated in the preceding section (page 103) that relative body width fails to show a dependence on growth rate within a population the differences between the two groups with respect to L/W can not be explained on the basis of differences in growth rate.

As was pointed out previously (page 82) the characters, L/D and L/DCP , show no apparent dependence on growth rate. Accordingly differences in growth rate can not be expected to explain the differences between the 1928 and 1929 year classes of the Muskellunge Lake cisco with respect to these characters.

The data of Table 52 furnish further and direct evidence that growth rate does not account for the differences between the 1928 and 1929 year classes with respect to the ratios L/W , L/D , and L/DCP . This evidence is obtained by the comparison of these body ratios in the II-group (1929 year class) and the III-group (1928 year class) for the intervals where the length frequencies of the two groups overlap (155 to 164 millimeters). If the three ratios under consideration have any dependence on growth rate it may be expected that II-group and III-group fish of the same length will show consistent differences with respect to them. The data of Table 52 show, however, that the values of L/D , L/DCP , and LW do not show consistently higher or lower values for either of the age groups over the short interval of overlap. This fact offers further evidence that differences between the 1931 collections of the 1928 and 1929 year classes with respect to L/W , L/D , and L/DCP do not depend on differences in the growth histories of the two groups.

The measurements of the interorbital width were made on the Muskellunge Lake cisco in order to provide a better knowledge of the proportions of the head. Since this measurement was not made on the specimens from Trout Lake, Silver Lake, and Clear Lake it is not possible to state conclusively whether the character, H/I , ordinarily has any dependence on growth rate. However, the fact that the



Figure 5. — Comparison of the typical appearance of the heads of the Muskellunge Lake cisco in individuals of the 1929 year class (at left) and the 1928 year class (at right).

values of H/I show no consistent tendency to change with length of fish in either of the Muskellunge Lake age groups (Table 52) may be taken as evidence that the relative size of the interorbital is not affected by growth rate.

Attention will now be given to the possibility that the structural differences between the 1928 and 1929 year classes of the Muskellunge

Lake cisco may represent different stages in a normal modification of body proportions with increase in length. Such an explanation may possibly apply to the differences in the characters, L/D , L/DCP , and L/W . If the variations in these three characters with length are examined (Table 52) there is detectable a tendency for each character to change in value according to length within the age groups.

The character, L/D , increases in value progressively in the II-group (1929 year class) from 4.00 at the 135—139 millimeter interval to 4.62 at the 155—159 millimeter interval. The end points are exceptions to this trend. In the III-group (1928 year class) L/D rises continuously from 4.62 at the 155-159 millimeter interval to 4.87 at the 170—174 millimeter interval. The last two intervals, however, show slight decreases in the value of L/D .

The variation of L/DCP in relation to length appears to be random and without trend in the II-group. In the III-group, however, where there are more specimens there is a distinctly noticeable trend for the ratio to increase as length increases.

The variation of L/W with length is irregular in the II-group, although there is possibly a very slight trend toward a rise in value with increase in length. In the III-group, however, the tendency for the ratio, L/W , to increase with increase in length is very strong. Only the final interval (180—184 millimeters) provides an exception.

Although the trends are not sharply indicated, it appears that the ratios, L/D , L/DCP , and L/W , all tend to increase in value with increase in body length. Such a progressive change of proportions might well account, at least in part, for the differences between the 1928 and 1929 year classes with respect to these characters. The differences, then, may depend only on differences in the average length of the two groups, and for this reason they cannot safely be considered to represent fundamental and permanent structural differences distinguishing the two groups.

The normal change of body proportions with length does not serve to explain the observed differences between the 1928 and 1929 year classes with respect to the characters L/H , H/E , L/E , and H/I , for where any tendency for these ratios to change with length within an age group is detectable, the direction of the change is opposite that which would be necessary to explain the differences between the two groups.

The variation of L/H , H/E , and L/E with length is without a detect-

able trend in the 1929 year class, but in the much better represented 1928 year class all three ratios show strong and consistent tendencies to increase in value with increase in body length. On the basis of these trends the 1928 year class, because it consists of the larger fish, would be expected to show the higher, not the lower, values for L/H , H/E , and L/E .

The value of H/I does not appear to have any dependence on length in either of the two year classes, and hence the differences between the two groups with respect to this character can not be explained as a consequence of the change of body proportions with length.

To summarize the preceding discussion, it may be stated that none of the differences showed by the 1928 and 1929 year classes of the Muskellunge Lake cisco for the characters listed in Table 52 can be explained as the result of differences in the growth rates of the two groups. The differences in the ratios, L/D , L/DCP , and L/W , may possibly be explained as the result of a regular and normal change of body proportions with length, but this explanation does not serve to explain the differences in the ratios, L/H , H/E , L/E , and H/I . It may be concluded, therefore, that the 1928 and 1929 year classes of the Muskellunge Lake cisco, as represented by the III-group and II-group, respectively, in the 1931 collection, exhibit significant and basic structural differences with respect to the relative values of head length, antero-posterior eye diameter, and interorbital width¹⁹). The most logical explanation of these differences lies in the assumption that they arose from differences in the environmental conditions at the time of the development and early growth of the cisco in the 1928 and 1929 seasons.

The presence of basic structural differences between the 1928 and 1929 year classes of the Muskellunge Lake cisco raises the interesting question as to which group approaches most nearly the normal condition for the population. Morphometric data on small collections of the 1930 and 1931 year classes, taken in 1932, throw some light on this question (Table 54). The comparison of Table 52 and Table 54 shows that of the four year classes the 1928 group shows the lowest values for the ratios (L/H , H/E , L/E , and H/I) with respect to which it was concluded that the 1928 and 1929 year classes exhibit significant and

¹⁹) The evidence of the 1932 collection, however, throws doubt on the existence of a difference between the two year classes with respect to the relative width of the interorbital. See page 113.

permanent differences. The relative head length of the 1929 year class is somewhat less than that of the 1930 year class, while members of the latter year class have relatively longer heads than the 1931 year class. If the antero-posterior diameter of the eye is considered in relation to head length the 1929 year class with a value of 3.95 for H/E has the relatively smallest eye, followed by the 1931 year class with a value, $H/E = 3.89$, and the 1930 year class with the value $H/E = 3.83$. If eye diameter is considered in relation to body length, L/E , the 1931 year class has the relatively smallest eye, followed by the 1929 and 1930 year classes in the order named. The average for H/I is largest in the 1929 year class followed in order by the 1930 year class and the 1931 year class.

Certain of the differences between the 1929, 1930, and 1931 year classes can be explained by differences in the growth rates of the specimens on which the morphometric averages were based (Table 53). The 1930 year class (1932 II-group) specimens show larger calculated average lengths than the 1929 year class (1931 II-group) at the end of both the first and second years of life, and were six millimeters longer at the time of capture in the third summer. From these facts it may be concluded that the specimens of the 1930 year class fish had a faster growth rate than those of the 1929 year class. It appears further that the growth rate of the 1931 year class fish (I-group of 1932) was faster than that of either the 1930 year class or 1929 year class fish. Not only is the calculated length at the end of the first year of life higher in the 1931 year class fish than in either of the other two groups, but the actual length of 139 millimeters at the time of capture in midsummer is greater than the total calculated length of the 1929 year class at the end of the second growth season and only a few millimeters less than the calculated length of the 1930 year class at the end of the second year of life²⁰).

By reason of their more rapid growth the 1931 year class specimens may be expected to have a larger average value of L/H than either the 1930 year class or the 1929 year class, while the 1930 year class may in turn be expected to have a larger value of L/H than the 1929 year class. The data (Tables 52 and 54) fit this expectation exactly. The relatively short head of the 1931 year class unquestionably contributed to the high average value of L/E in that group. It will be

²⁰) This rapid growth of the I-group specimens is probably the result of the selective action of the gillnets used in taking the specimens.

noticed, however, that in spite of the shorter head of the 1930 year class as compared to the 1929 year class, the latter group has the higher value of L/E . This apparent disagreement is explained by the lower value of H/E in the 1930 year class.

If the comparison of the morphometric characters of the four year classes is considered as a whole, it appears that the 1929, 1930, and 1931 year classes resemble each other rather closely while the 1928 year class is distinct from any of them. From this it may be concluded that the morphological differences between the 1928 and 1929 year classes may be considered the result of a deviation of the former group from the conditions normal for the Muskellunge Lake cisco population.

The effect of the presence of the large-eyed 1928 year class in the 1931 collection from Muskellunge Lake on the determination of the relative size of the eye and particularly on the comparison of the Muskellunge Lake cisco with the Trout Lake cisco is showed in the data of Table 55. First it may be pointed out that on the basis of data for the 1929, 1930, and 1931 year classes the Muskellunge Lake cisco would be expected normally to show values of approximately 16.8 and 3.90 for L/E and H/E , respectively. Thus the antero-posterior diameter of the eye in the Muskellunge Lake cisco would be distinctly smaller than that of the Trout Lake cisco in relation to total length and slightly smaller in relation to head length. However, the presence of the 1928 year class in the 1931 Muskellunge Lake collection reduced greatly the differences between the Trout Lake cisco and the Muskellunge Lake cisco in the ratio L/E and reversed the positions of the two stocks with respect to the ratio H/E . As a result a natural growth relationship, namely, the dependence of eye size on growth rate, was obscured. Although the four cisco populations of this study showed a correspondence in their arrangement with respect to growth rate and the ratio L/E , the presence of the large-eyed 1928 year class in the Muskellunge Lake collection prevented the appearance of such a correlation between growth rate and the ratio, H/E (page 85).

In order to obtain further information on the structural differences between the 1928 and 1929 year classes of the Muskellunge Lake cisco a large collection of 795 specimens was taken in the summer of 1932.

The preliminary examination of the 1932 collections from Muskellunge Lake revealed the continued presence of both the large-eyed and the small-eyed individuals. The 1932 sample differed from the 1931 sample, however, in certain respects. The small-eyed individuals

were somewhat more slender than in the preceding year. Whereas in the 1931 collections the small-eyed fish had been noticeably smaller than the large-eyed ones, in 1932 the small-eyed fish were on the average only slightly smaller than the large-eyed individuals. The 1932 sample was characterized also by the presence of several rather small fish, most of which had relatively small eyes.

The observations of the preceding paragraph suggest that the following changes may have occurred in the Muskellunge Lake population: (1) The normal decrease in body depth with increase in length caused the 1929 year class fish to be slenderer in 1932 than in 1931; (2) the growth of the 1929 year class from 1931 to 1932 was superior to that of the 1928 year class with the result that in 1932 the two year classes were no longer separable into two distinct length groups (see Table 56); (3) individuals of year classes not occurring in the 1931 collection were of sufficient size to be taken in 1932 — these new year classes resembled the 1929 year class in the possession of relatively small eyes.

The examination of scales made it apparent that the 1932 collection would be of limited value in the study of the morphological differences between the year classes of 1928 and 1929. The I-group and the II-group individuals could be identified easily²¹⁾ but the separation of the III-group from the IV-group could not be accomplished with any degree of satisfaction or certainty. Although the fourth annulus was only rarely completely formed, the scales of many specimens showed a partial formation of a fourth annulus. The possibility is thus suggested that in some instances the individuals of the 1928 year class may have formed no annulus at all at the end of the fourth year²²⁾ The situation is confused further by the fact that accessory annuli are of regular occurrence in the Muskellunge Lake cisco. In young fish these summer checks offer no special difficulty, but in the later years, when the true annuli are crowded together, the false annuli often render a scale wholly unreadable.

Scale examinations were made for 201 of the 795 preserved specimens in the 1932 Muskellunge Lake cisco collection. Fifteen of these fish were members of the I-group (1931 year class) and 24 were members of the II-group (1930 year class). Of the remainder 75 were assigned to the III-group (1929 year class) and 74 to the IV-group (1928 year class). It is probable that the age deter-

²¹⁾ The morphometric data for the 1932 I-group and II-group of the 1932 Muskellunge Lake cisco collections are showed in Table 54.

²²⁾ Olofsson (1932) mentioned that with exceptionally slow growth coregonids may fail to lay down distinct year marks.

minations of practically all of the 74 fish assigned to the IV-group were correct. Although the formation of the fourth annulus was incomplete in many of them, all gave positive indication that an annulus, complete or partial, was definitely present. On the other hand the accuracy of the age determinations for the 75 fish assigned to the III-group is questionable, for it is quite possible that these supposedly III-group fish may have included numerous IV-group individuals that failed to form even a partial fourth annulus. It will be seen that the morphometric data of the following pages support the suspicion that the age determinations of many of the fish assigned to the III-group in the 1932 collection were erroneous.

In Table 57 may be found a comparison of the average values for the characters, L/H, L/E, H/E, and H/I, for the 1928 and 1929 year classes in the 1931 and the 1932 collections. (These are the characters with respect to which a permanent difference between the year classes was indicated by the 1931 data.) The 1931 and 1932 data for the 1928 year class show almost perfect agreement for the ratios, L/H, H/E, and L/E. The average for H/I, however, is definitely higher in the 1932 fish. The 1931 and 1932 data for the 1929 year class, however, fail to show the same close agreement observed in the data for the 1928 year class. Although the ratio, L/H, is practically the same in the two years' collections of the 1929 year class, the ratios showing the relative size of the eye (H/E and L/E), while distinctly higher than the corresponding ratios for the 1928 year class, are considerably lower in the 1932 than in the 1931 material. These decreases in the average values of L/E and H/E in the 1929 year class data are precisely what might be expected if, as was suggested, part of the 1932 fish assigned to the III-group were actually members of the IV-group. A similar explanation might account also for the drop in the value of H/I.

Although the erroneous assignment of IV-group individuals in the III-group might well explain the lower value of H/I in the 1932 (III-group) sample of the 1929 year class, it is difficult to explain the increase of H/I in the 1928 year class from the 1931 to the 1932 sample. If it could be assumed that all the erroneously aged IV-group fish were individuals with low values of H/I, while those aged correctly had large values of H/I the difficulty might possibly be circumvented. However, there appears to be no sound basis for correlating a low value of H/I with the failure to form an annulus; consequently it must be held that the 1932 data throw in doubt the existence of any significant differences between the 1928 and 1929 year classes in the relative width of the interorbital. (See page 116.)

The examination of the variation of body ratios, L/H, L/E, H/E, and H/I, with length within an age group throws further light on the question of the possible effect of erroneous age determination on the averages for these ratios in the 1932 sample of the 1929 year class. (Table 58.)

In the 1929 year class (III-group) a very high value of L/H occurs at the modal length frequency interval (160—164 millimeters). Expect for the single individual at 175—179 millimeters, L/H is smaller for fish at all lengths on either side of this modal interval. In the 1928 year class sample (IV-group) L/H drops slightly from the 155—159 millimeter interval to the 165—169 millimeter interval and then increases rather sharply up to the 180—184 millimeter interval. In spite of the irregularities it may be said that in the 1928 year class sample L/H shows a slight tendency to increase with increase in the length of fish.

The ratio L/E shows a slight tendency to increase in value over the lower length intervals of the 1929 year class but then drops suddenly between the 160—164 millimeter interval and the 165 to 169 millimeter interval. If the 1929 year class material is considered as a whole, it may be stated that the longer fish tend to have lower average values of L/E than the shorter ones. In the 1928 year class data, however, L/E does not show any similar tendency to decrease with increase of fish length, but, on the contrary, shows a pronounced and consistent trend toward an increase with increase in the length of the fish.

The value of H/E shows a fairly consistent decrease with increase in fish length in the 1929 year class data. The changes of the same ratio are more irregular in the 1928 year class, but the general tendency is for H/E to increase with increase in the length of the fish.

The longer fish of the 1929 year class sample show, on the average, a slightly lower value of H/I than shorter ones. However, the irregularity in the variation of the ratio is so great that it is probably not valid to speak of any general trend. The two lowest length intervals of the 1928 year class sample (155—165 millimeters) show distinctly the lowest average values for H/I . However, the highest average value of H/I in a well represented length interval (4.07 at 165—169 millimeters) also occurs at one of the lower length intervals. Consequently, it can not be held that there is any marked trend in the change of H/I with change in fish length in the 1928 year class.

If the variation of body ratios with fish length in the 1932 data (Table 58) is compared with the corresponding data for 1931 (Table 52), it may be seen first that the two years' samples of the 1928 year class show good agreement. In both the 1931 and 1932 collections of this year class the ratios L/H , L/E , and H/E show distinct tendencies to

increase in value with increase in the length of the fish, while no distinct trend in the changes of H/I is discernible in either sample.

The small number of specimens (29) in the 1931 collection of the 1929 year class is not adequate to show clearly any trends in the change of body ratios with increase in the length of the fish. There is, however, strong evidence for disagreement between the 1931 and 1932 data of the 1929 year class. Although the samples of both years agree in showing irregular variation of L/H and H/I , the sharp tendency, apparent in the 1932 data, for the longer fish to have the relatively larger eyes is not to be found in the 1931 data.

The changes of L/H , H/E , and L/E with increase of length of fish in the 1928 year class samples of both 1931 and 1932 are a natural consequence of the dependence of these characters on growth rate, for it was demonstrated in the preceding section that the more rapidly growing fish of an age group show a strong tendency to have shorter heads and smaller eyes than the more slowly growing fish of the same age group. The 1931 collection of the 1929 year class is too small to be held either in agreement or disagreement with this generally existant tendency. In the 1932 data of the 1929 year class, however, the changes of L/H , H/E , and L/E either fail to fulfill the expected tendencies or run absolutely counter to them. The ratio, L/H , shows little or no tendency to increase with increase in the length of the fish while L/E and H/E show strong tendencies to decrease with increase in the length of the fish.

The erroneous assignment of IV-group (1928 year class) fish to the III-group (1929 year class) offers a reasonable and satisfactory explanation for the failure of the individuals of the 1932 collection of the 1929 year class to show the expected dependence of head length and eye diameter on growth rate. Since the 1928 year class individuals have longer heads and larger eyes than those of the 1929 year class the erroneous inclusion of members of the former group in the 1929 year class sample may be expected to lower the values of L/H , H/E and L/E in the data for this latter group. Further, the effect of such erroneous age determinations would be expected to be greatest at the lengths of fish at which the IV-group (1928 year class) is most abundant. The data of Table 58 show that the most pronounced decreases in the values of these ratios in the 1929 year-class data are actually to be found at the lengths at which the IV-group or 1928 year class fish are most numerous. Not only does the erroneous inclusion of 1928 year

class fish in the data for the 1929 year class of the 1932 collection explain the decrease of H/E and L/E with increase in length and the failure of L/H to show definite increase with increase in length; it accounts also for the fact that L/E and H/E have lower average values in the 1932 data for the 1929 year class than in the 1931 data for the same group. In view of the preceding considerations it is valid to state definitely that the differences between the 1928 and 1929 year classes in relative head length and eye diameter observed in the 1931 collection persisted with little change in the 1932 collection.

Attention should be called to the fact that the average for L/H in the 1932 data of the 1929 year class is slightly higher than in the 1931 data. This situation is contrary to expectation since the erroneous inclusion of 1928 year class fish in the 1929 year class sample would be expected to cause L/H to be lower in 1932 than in 1931. It is of course possible that the 1931 average, based on only 29 fish, was slightly too low, or it may be that the average relative head size of the 1929 year class actually underwent slight change between 1931 and 1932. Regardless of the causes of this discrepancy, it does not throw in doubt the conclusion that significant differences between the 1928 and 1929 year classes in the relative size of the head were present in 1932 as well as in 1931.

The data of Table 58 offer no satisfactory explanation of the differences between the 1931 and 1932 data with respect to the ratio, H/I . It is quite true that the erroneous inclusion of IV-group individuals (1928 year class) in the 1932 III-group (1929 year class) might well explain the decrease of H/I in the latter year class from 1931 to 1932. This explanation, however, fails to account for the increase from 1931 to 1932 in the value of H/I in the 1928 year class, unless, as mentioned previously (page 113), it is assumed that in the 1932 IV-group a low value of H/I was associated with failure to form the fourth annulus. The data of Table 58 show that such an assumption is untenable. The scarcity of III-group fish at the higher lengths indicates that almost all the longer IV-group fish formed annuli and hence were aged correctly. Nevertheless, the value of H/I is as high in these longer IV-group fish as it is in the shorter ones. Nor do the 1929 year class data for H/I show the continued decrease with increase in length that might be expected if the 1928 year class fish actually had lower values of the ratio than the 1929 year class. It must be concluded therefore

that in 1932 the 1928 and 1929 year classes had no significant differences with respect to the relative width of the interorbital.

Although the ratios, L/H, H/E, L/E, H/I, L/D, and L/DCP, were determined for each of the 795 Muskellunge Lake ciscoes collected in 1932, it was felt that an attempt to determine the ages of all the fish in this large collection would not yield results more conclusive than those obtained from a sample of 201 fish. The data for the entire collection were, however, compiled to show the average value for each of the six body ratios for each five millimeter length interval (Table 59). Because of the fact that all ages from the I-group to the IV-group were represented in the 1932 collection it is not possible to make reliable estimates of the age composition at different lengths. However, the comparison of Table 58 and Table 59 does not give any indication that the use of more than 201 specimens would have changed any of the conclusions based on the former table.

If the data of the 1931 and 1932 cisco collection from Muskellunge Lake are considered as a whole, it is valid to state that the 1928 and 1929 year classes show real and persistent differences. The two groups show differences in general appearance, in the size of the head, in the pigmentation of the body, and particularly in the relative size of the eye. While they are definitely unlike with respect to yet other characters (for example, relative body depths) the question of change of form with length renders these differences of doubtful significance. In contrast to the above mentioned differences between the two year-classes attention should be called to their extraordinarily close agreement with respect to other characters, particularly the numerical characters (See Tables 6 and 10). The two groups appear to be similar in habit. They do not segregate themselves within the lake, but are taken together in the nets regardless of locality or depth²³). As stated before (page 109) the most logical explanation for the structural differences between them is that they found their origin in the nature of the environmental conditions at the time of hatching and early development.

²³) When the presence of two cisco types was first detected in Muskellunge Lake, it was suspected that there might be two distinct races in the lake. However, the identical distribution in the lake, the similar growth, and especially the fact that all fish of the larger eye type were members of the 1928 year class while all fish of the small eye type were of the 1929 year class eliminated any possibility that the differences might be racial.

In the populations of the other lakes the samples show certain differences to exist between year classes (Tables 5 to 7 and 9 to 12). On the whole these differences can be traced to the small size of the samples representing the particular year-groups or to the changes of body proportion with increase in length. There is, however, one example of an apparently significant difference between two year classes with respect to a numerical character, the number of gillrakers on the first branchial arch. In the Silver Lake collection the 38 specimens of the III-group gave an average gillraker count of 45.84 with a probable error of ± 0.22 , while the 70 specimens of the V-group gave the value 44.53 ± 0.16 . The frequency distribution of the raker number in the two groups may be seen in Table 60. The difference between the two averages is 1.31 and the probable error of the difference is ± 0.27 . Since the probable error of the difference is contained 4.9 times in the difference between the means, it is quite possible the difference is significant.

If it be considered that the observed fundamental differences between different year classes in the same population arise from differences in the environmental conditions at the time of development, it is by no means surprising to find great differences between the populations of neighboring but dissimilar lakes. It appears probable further that much of the present elaborate systematic division of the many inland lakes cisco populations (Koelz 1931) may be based on differences that are not genetic but are environmental in origin.

The systematics of *Leucichthys artedi*.

The only comprehensive survey of the forms of the lake herring or cisco, *Leucichthys artedi*, is that published by Koelz (1931). In this publication Koelz named seventeen new subspecies of *artedi* which, together with typical *artedi* and previously described forms, brought the number of recognized subspecies to a total of twenty-four. Because of the rather strong evidence that such an elaborate systematization of the numerous forms of *L. artedi* may have been to a considerable extent premature, a brief general consideration of the systematic problems presented by this species will be undertaken.

Any discussion of the relationship of the members of a systematic group must inevitably include a consideration of the problem of the origin of the various forms. The geological history of the region in which *L. artedi* now occurs makes it apparent that the members of

the species came to occupy their present habitats subsequent to the last glacial period. The taxonomic problems of the group would be greatly simplified if it could be assumed that all the present forms had been fully differentiated prior to the time of the last glacier, and that the recolonization that followed the recession of the ice sheet represented merely a selection by each form of its most favored and most suitable habitat. Such an assumption, however, does not appear to be reasonable. In addition to *artedi* with its twenty four subspecies, there are listed in modern literature no less than nine other species of the genus *Leucichthys*, and several of these nine include recognized subspecies. Obviously all these *Leucichthys* forms are closely related; it is difficult to determine even the species of many individuals in the genus. In view of these very close affinities of the many recognized forms, it would scarcely appear plausible to assume that they all existed in the glacial waters of the past as so many well differentiated and distinct groups. It appears on the whole more logical and valid to assume that much of the differentiation that has led to the present great number of forms occurred since the withdrawal of the last ice sheet.

Discussion of the course of differentiation in *artedi* and of the factors that contributed to it must rest largely on a speculative basis. There is no means of determining now, just how far the differentiation of the present forms had proceeded when they first occupied their present habitats. As has been pointed out, it is likely that many of them did not possess the appearance and characteristics they show today. On the other hand, it is quite within the range of probability that these early ancestors of the modern forms of *artedi*, at the time of their redistribution, may have already been differentiated into several basic types, separated by physiological or ecological barriers.

In the differentiation of the single stocks in the various lakes, isolation must have played an important rôle. Many of the differences to be observed among the numerous cisco stocks are unquestionably genetic, but the difficulty of discrimination between these genetic differences and those which have resulted from the direct modifying influence of the environments is great. This problem of distinguishing between genetic and non-genetic characters is fundamental to the solution of the problem of the systematics of *L. artedi*. Since the function of taxonomy is the elucidation of phylogenetic relationships, no sound system of classification can be based on the use of characters

that change according to the direct effect of the environment on the individual. Systematic zoologists have in general recognized the importance of basing their classifications on purely genetic characters. While in most groups the problem of extensive non-genetic modifications is not a source of very great difficulty, the extreme plasticity of the coregonids²⁴) is such that the actual taxonomic worth of even pronounced differences may at times be questionable.

The problems relative to the systematics of *L. artedi* can be illustrated by an examination of the basis for the separation of several of its subspecies in the light of the available data on the modifying effects of the environment and on the range of variation within single populations. The lakes whose cisco populations formed the basis of the present study all lie in Vilas and Oneida Counties, Wisconsin. From these same counties Koelz (1931) recorded, in addition to *clarensis* and *clemensi*, five other subspecies of *artedi*. Table 61 shows the morphological characters for each of the seven subspecies as indicated in Koelz' key for the analysis of the subspecies of *artedi*. While it is admitted that the transcribing of this material from a key into a tabular form fails to bring out the intended logical arrangement of the twenty-four subspecies, it is also apparent that the separation of several of these seven subspecies is based on the slenderest of differences. With respect to the gillrakers only *wagneri* is clearly separated from the other groups, and this subspecies was described from only nine specimens. As concerns the lateral line scales, little significance can be ascribed to the indicated differences in this character, that may show a range of variation of 20 to 25 or even more scales within a single population. Relative body depth is also of questionable value as a basis of separation, for it was showed in an earlier section of this publication that this ratio may vary tremendously with age, and further that the change with age may proceed in opposite directions in different populations that had been assigned to the same subspecies. The data of the present study also throw into doubt any separation of the subspecies on the basis of the relative length of the maxillary. Table 61 shows no real differences in maxillary length among the subspecies *atikamek*, *artedi*, *clemensi*, *lowei*, and *woodi*. However, both *clarensis* and *wagneri* are indicated to have a slightly shorter maxillary than the remaining five subspecies. Nevertheless, this investigation

²⁴) Woltereck (1932) pointed out that systematic problems similar to those encountered in the coregonids occur also in the snails and cladocerans.

has showed that not only is there an apparent relation between length of maxillary and rate of growth, but also that the slow-growing populations of Silver and Muskellunge lakes, referred by Koelz to *clarensis*, resemble the slow-growing Trout Lake *clemensi* stock in the relative length of the maxillary more closely than they resemble the rapidly growing *clarensis* type form of Clear Lake. The small indicated differences among the subspecies as to the relative length of the snout also fail to convince, particularly in view of the great variability of this character not only within a single population but also from one population to another. Finally the use of the ratio PV/P is open to the serious objection that the indicated values were presented without reference to sex differences in the size of the paired fins.

Such indefinite separations are by no means confined to the seven subspecies which were just considered. The same key from which the data of Table 61 were drawn includes numerous similar examples. As illustrations, *greeleyi* and *huronius* are separated by reason of values of H/S less than 4.1 in the former and 3.9—4.2 in the latter, while *artedi* and *osmeriformus* differ in gillraker numbers that are „46—51 but frequently fewer“ in the former and „47—51 but often more“ in the latter.

It is quite obvious that classifications on such standards as have been used for the separation of the subspecies of *artedi* would require that the population of each lake included in the present study be considered as a subspecies distinct from each of the other populations. The same standards, applied rigorously and without reference to the source of the material, would require also a systematic separation of the juvenile and adult forms of the Clear Lake cisco, of the 1928 and 1929 year classes of the Muskellunge Lake cisco, and possibly of the 1926 and 1928 year classes of the Silver Lake cisco. This final *reductio ad absurdum* makes the conclusion inescapable that the present elaborate systematization of the species *artedi* is in large measure without demonstrated validity.

The preceding discussion is not intended to imply that no genetic differences exist between the various *artedi* forms. The long isolation of many of them in their own peculiar and special environments must have been most favorable for the origin and preservation of genetic differences among the several stocks. The detection of these genetic differences and the determination of their extent and significance, however, provide a problem of exceptional difficulty. The experience

of continued analytic investigations may show whether the problem can be brought to any satisfactory solution. Transplantation experiments promise to be more critically valuable. However, pending the accumulation of adequate data for a separation of the *artedi* forms according to their true and natural relationships, it would appear that the designation of a local form can be made best through a description of its salient characters and a recording of the locality it inhabits.

Although the above conclusions are based on the study of *L. artedi* alone, and hence in their specific applications must be confined to this single species, it should be pointed out that several European investigators of essentially parallel situations have arrived at closely similar conclusions. These European investigations have been discussed previously in the section on „Variation in the Coregonids“, but some of them may well be mentioned again here. Otterstrøm (1922) held that the brackish water and fresh water forms of *C. lavaretus* in Denmark are not systematically distinct but represent only biological forms. Kulmatycki's (1926, 1927) extensive studies of coregonids in Poland led him to include all Polish forms of the subgenus *Coregonus* under the single species, *C. lavaretus*. Kreitmann (1929, 1931) emphasized the utter futility of attempting to divide coregonids into species or subspecies. Monti (1929, 1930, 1933) concluded that the many forms of Italian coregonids are not subject to classification in terms of species, subspecies, or even distinct races. Thus it appears that the problems of coregonid taxonomy are in general the same in Europe and North America. Consequently the data and conclusions that have been presented here with specific reference to the systematics of *L. artedi* may be held to possess a certain degree of significance with respect to the general problem of coregonid taxonomy.

Summary and conclusions.

1. The present study of the morphometry of the cisco populations of Trout Lake, Muskellunge Lake, Silver Lake, and Clear Lake in the highland lake district of northeastern Wisconsin, is based on a total of 1,548 specimens collected in the summers of 1931 and 1932. Of this number 753 were used in the general investigation of the morphological characteristics of the four stocks, while the 795 fish taken from Muskellunge Lake in 1932 were employed in a special study of morphological differences between the 1928 and 1929 year classes in that lake.

2. As a preliminary to the present study a short review of the present status of the problem of variation in the coregonids was presented.

3. Since this investigation is concerned in part with the question of the relationship between growth rate and body form, a brief review was presented of the growth histories of each of the four populations. This review was based on the data of Hile's (1936) study of the growth of these same populations.

4. Data were presented to show for each population: (a) the range, distribution, and average value for the entire sample for each of the 18 body ratios and 9 numerical characters considered; (b) the differences between age-groups in the average values of the body ratios; (c) the differences between year classes in the values of the numerical characters; (d) the change with length of the body ratios that showed distinct tendencies to change with age.

5. Most of the morphological characters show such a wide range of variation within a single population that reliable average values can be obtained only by the use of very large samples.

6. The four populations showed themselves to be distinct each from all the others. The three populations (from Muskellunge Lake, Silver Lake, and Clear Lake) assigned by Koelz (1931) to the subspecies, *clarensis*, differed as much among themselves as they did from the Trout Lake population assigned by the same author to the subspecies, *clemensi*. Further, these populations assigned to the same subspecies showed differences as great as or greater than those which now separate some of the subspecies of *L. artedi*.

7. Certain of the body ratios showed a distinct tendency to change with increase in length and age. The direction of change with respect to a single character was not always the same in all the populations. Ratios that showed a tendency to change with increase in length and age were: L/D, L/DCP, L/W, D/E, PV/P, AV/V. The ratio, L/H, showed a distinct tendency to decrease with age, but showed no corresponding tendency to decrease with increase in length, independent of age.

8. With respect to the average values of some of the body ratios the populations arranged themselves in the order of their growth rates. The ratios that showed such a relation to growth rates were: L/H, L/W, L/E, H/M, PV/P, AV/V, DH/DB. The arrangement was such that the population with the more rapid growth had the shorter

head, maxillary, paired fins, and dorsal fin, the wider body, and the smaller eye diameter.

9. Analysis of individual populations with respect to the seven body ratios whose values showed an apparent correlation with growth rate revealed that within a single population there is a certain degree of dependence of individual relative head length, eye diameter, maxillary length, and fin length on individual growth rate. This dependence is particularly strong with respect to relative head length and eye diameter. The variations in relative body width within a population did not indicate any dependence of individual relative body width on individual growth rate.

10. At all ages beyond the second or third year the males had relatively longer paired fins than the females. The only other sex differences detected were in the Clear Lake cisco where the females had the higher values of L/H and L/E , and the lower values for L/W and L/D . The shorter head and lesser eye diameter (in relation to total length) of the Clear Lake females depend in large measure on the fact that the females of this population grow more rapidly in length than the males.

11. The 1928 and 1929 year classes of the 1931 collection of the Muskellunge Lake cisco showed mathematically significant differences in the ratios L/H , L/E , H/E , L/D , L/DCP , L/W , and H/I . None of the differences can be explained on the basis of differences in the growth rates of the two groups. The differences between the two year classes in relative body depth, depth of the peduncle, and relative body width may be explained in part, at least, as different stages in a normal change of body proportions with increase in length. The data for the 1932 collection of the Muskellunge Lake cisco showed no differences between the 1928 and 1929 year classes with respect to H/I but showed a persistence of the differences between the two groups with respect to relative head length and eye diameter. It was concluded, therefore, that the 1928 and 1929 year classes of the Muskellunge Lake cisco exhibit basic and permanent differences with respect to head length and eye diameter. In fresh specimens the 1928 year class fish showed a distinctly darker pigmentation in the dorsal region than the 1929 year class fish.

12. It was suggested that the permanent morphological differences between the 1928 and 1929 year classes of the Muskellunge Lake cisco may be the result of differences in the environmental conditions in

the two calendar years at the time of development and early growth of the cisco.

13. Comparisons of the 1928 and 1929 year classes of the Muskegon Lake cisco with small samples of the 1930 and 1931 year classes indicated that the differences between the two groups first named may represent a deviation of the 1928 year class from conditions normal for the population.

14. The 1926 and 1928 year classes of the Silver Lake population furnished a single example of a probably significant difference in gillraker number between two year classes of the same population.

15. In a discussion of problems relative to the systematics of *Leucichthys artedi* it was held that the present elaborate division of the species into twenty-four subspecies is to a large extent invalid because:

(1) The differences upon which the separations of the subspecies have been based are too slight and indefinite in comparison with the wide range of natural variation of the characters used.

(2) The values of certain characters that have been used in the separation of the subspecies show a distinct dependence on growth rate.

(3) Natural changes of body proportion with increase in length and age produce greater differences between fish of different length in the same population than those that have been employed in the separation of some subspecies.

(4) Permanent morphological differences between different year classes of the same population may be more extensive than the recorded differences between subspecies.

(5) Separations of subspecies on the basis of the relative lengths of the pectoral and ventral fins have been made without regard for sex differences in these characters.

16. Attention was called to the need of extensive analytical and experimental investigations to determine the true range of natural variation and the actual degree of plasticity of the cisco. Until such investigations may make possible a clearer conception of the true relationships among the many forms of the cisco, the present subspecific terminology may well be abandoned and the designation of any particular population confined to a statement of its morphological characteristics and a record of the locality in which it occurs.

Appendix.

Morphometry of the Palette Lake cisco.

A collection of eighteen ciscoes was made in Palette Lake, July 21 and 22, 1931. The specimens, including eleven males and seven females, ranged in length from 140 millimeters to 214 millimeters. They were measured and their numerical characters counted after the methods employed in the preceding morphometric investigation. The general results of the examination of this small collection of Palette Lake ciscoes appear in Table 1 which shows the maximum, the mean, and the minimum value for each character considered.

Table I. — *Maximum, mean and minimum value for each of the morphological characters investigated in the Palette Lake cisco.*

Character	Maximum value	Mean value	Minimum value	Character	Maximum value	Mean value	Minimum value
L/H	4.68	4.48	4.21	PV/P ♂ .	2.00	1.83	1.68
L/D	4.80	4.44	4.18	♀ .	2.22	1.94	1.81
L/W ...	9.62	8.27	7.15	AV/V ♂ .	1.84	1.68	1.54
L/AT ...	8.58	7.56	6.79	♀ .	1.96	1.78	1.67
L/DCP ..	15.53	13.30	11.92	DH/DB .	1.61	1.45	1.33
L/DB ..	10.20	9.16	8.32	R 47	45.2	44	
L/AN ..	9.85	9.20	8.16	Sc 87	80.2	76	
L/AD ..	15.85	13.72	11.88	RD 8.5	7.9	7.5	
L/PV ...	3.73	3.41	3.12	RC 25	23.9	23	
L/E	22.59	18.18	15.61	BR 9	9.0	9	
PV/AV ..	1.17	1.09	1.01	DR 12	11.9	11	
H/S	4.73	4.36	4.00	AR 14	12.8	11	
H/E	4.82	4.06	3.55	PR 16	15.3	14	
H/M ...	3.54	3.11	2.87	VR 12	11.9	11	
D/E	4.75	4.09	3.67				

Koelz (1931) examined a collection of twenty-eight specimens of the Palette Lake cisco, and assigned this population to the subspecies *clarensis*. Concerning this population he stated, „the race has the short snout and maxillary characteristic of *clarensis*, but the head tends to be relatively small, approaching *sisco*“. The present small collection, however, indicates that the relative head size of the Palette Lake cisco is almost identical with that of the race from the type locality, Clear Lake.

This small collection of ciscoes from Palette Lake is of particular interest here because of the further light it throws on the question of the relationship between the values of certain morphological characters and the rate of growth. Although the study of the age and growth of the cisco in northeastern Wisconsin (Hile, 1936) included no material from the Palette Lake cisco population there are available certain data relative to the growth of this population. Dr. Stillman Wright, formerly of the Bureau of Fisheries, examined the scales of 145 individuals collected in 1928. Of this number he was able to read 100 or about 69 per cent. The remainder were discarded as unreadable. The difficulties encountered in the determination of individual ages depended almost entirely on the crowding together of the annuli in the later years of life. The available growth data can, however, be considered reliable up to the end of the third year. (I have examined scales from Palette Lake ciscoes, and find no occasion to disagree with Dr. Wright.)

According to Dr. Wright's data the average length of the Palette Lake cisco at the end of the first year of life is 100 millimeters; at the end of the second year it is 169 millimeters; and at the end of the third, 186 millimeters. From these data it appears that growth in the Palette Lake cisco is definitely greater than that in the Muskellunge Lake and Silver Lake stocks and less than that in the Clear Lake population. It might be expected then that, with respect to characters affected by growth rate, the Palette Lake cisco would show values intermediate between those of the Clear Lake cisco and those of the Silver Lake and Muskellunge Lake fish.

Table II shows the relationship of the Palette Lake cisco to those of Trout, Muskellunge, Silver, and Clear lakes, with respect to morphometric characters that appear to be correlated with growth rate. The scheme of comparison is based on the assignment of the value 1.00 to the smallest value for a particular character showed by any lake. The values of the same character in the remaining lakes are expressed as factors of the smallest value (see page 90). If the small number of specimens is considered it can be said that the values of morphological characters in the Palette Lake cisco fit nicely into the arrangement of the populations on the basis of growth rate.

Table II. — *Relative positions of five cisco populations with respect to the average values for morphological characters that appear to be correlated with growth rate.*

Character	Trout	Muskellunge	Silver	Palette	Clear
L/H	1.00	1.09	1.14	1.16	1.17
L/W	1.38	1.35	1.28	1.24	1.00
L/E	1.00	1.05	1.25	1.23	1.44
PV/P ♂	1.00	1.10	1.10	1.11	1.24
♀	1.00	1.09	1.15	1.13	1.26
AV/V ♂	1.00	1.11	1.07	1.13	1.26
♀	1.00	1.13	1.11	1.14	1.29
DH/DB	1.34	1.18	1.18	1.11	1.00
H/M	1.00	1.07	1.06	1.06	1.16
RD	1.00	1.06	1.06	1.10	1.18
RC	1.00	1.06	1.04	1.15	1.17

Bibliography.

- Bajkov, Alexander**, 1933. Description of two new whitefish from Manitoban waters. Internationale Revue der gesamten Hydrobiologie und Hydrographie. Bd. 29, Heft 1/2, 1933, S. 29—32. Leipzig.
- Bauer, Victor**, 1927, Die Felchen des Laacher Sees. Zoologischer Anzeiger. Bd. 74, 1927, S. 167—181. Leipzig.
- Dymond, John R.**, 1926, The fishes of Lake Nipigon. University of Toronto Studies, Biological Series No. 27, Publications of the Ontario Fisheries Research Laboratory, No. 27, 1926, pp. 1—108. Toronto.
- Dymond, John R.**, and **John L. Hart**, 1927, The fishes of Lake Abitibi (Ontario) and adjacent waters. University of Toronto Studies, Biological Series No. 29, Publications of the Ontario Fisheries Research Laboratory, No. 28, 1927, pp. 1—19. Toronto.
- Fatio, V.**, 1890, Faune des vertébrés de la Suisse. Histoire naturelle des Poissons. Vol. V, II^{me} Partie, 1890, pp. LXXX + 1—576. Genève et Bâle H. Georg.
- Freidenfelt, T.**, 1934, Untersuchungen über die Coregonen des Wenersees. Internationale Revue der gesamten Hydrobiologie und Hydrographie. Bd. 30, Heft 1/2, 1934, S. 49—163. Leipzig.
- Greeley, John R.**, 1934, Fishes of the Raquette Watershed. A Biological Survey of the Raquette Watershed, Supplemental to Twenty-third Annual Report 1933 (1934), State of New York, Conservation Department, 1934, pp. 53—108. Albany.
- Hart, John Lawson**, 1931, The growth of the whitefish, *Coregonus clupeaformis* (Mitchill). Contributions to Canadian Biology and Fisheries, being studies from the Biological Stations of Canada, New Series. Vol. VI, No. 20 (Series A, General, No. 5), 1931, pp. 429—444. Toronto.

- Hile, Ralph**, 1936, Age and growth of the cisco *Leucichthys artedi* (Le Sueur), in the lakes of the northeastern highlands, Wisconsin. Bulletin of the Bureau of Fisheries, Vol. XLVIII, p. 211—317, Washington, D. C.
- Hubbs, Carl L.**, 1926, The structural consequences of modifications of the developmental rate in fishes, considered in reference to certain problems of evolution. The American Naturalist, Vol. LX, 1926, pp. 57—81. New York.
- Hubbs, Carl L.**, 1934, Racial and individual variation in animals, especially fishes. American Naturalist. Vol. 68, 1934, pp. 115—128. New York.
- Järvi, T. H.**, 1928, Über die Arten und Formen der Coregonen S. Str. in Finnland. Acta Zoologica Fennica 5, 1928, pp. 1—259. Helsinki.
- Koelz, Walter N.**, 1929, Coregonid fishes of the Great Lakes. Bulletin, Bureau of Fisheries. Vol. XLIII, Part II, Document No. 1048, 1929, pp. 297—643. Washington.
- Koelz, Walter N.**, 1931, The coregonid fishes of northeastern America. Papers of the Michigan Academy of Science, Arts, and Letters. Vol. XIII, 1930 (1931), pp. 303—432. Ann Arbor.
- Kreitmann, Louis**, 1929, L'acclimatation du lavaret du Bourget dans le Lac Lemman et sa relation avec la systématique des Corégones. Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie. 1929, Bd. IV, S. 415—434. Roma.
- Kreitmann, Louis**, 1931, Travaux récents sur les corégones. Bulletin Français de Pisciculture. Quatrième Année, Nr. 40, 1931, pp. 102—108. Orléans.
- Kulmatycki, Wladimir**, 1926—1927, Studien an Coregonen Polens. Archives d'Hydrobiologie et d'Ichthyologie. Tome I, Nr. 4, 1926, pp. 276—336, et Tome II, Nr. 1, 1927, pp. 1—40. Warsaw.
- Lechler, Hermann**, 1930, Untersuchungen über den Kröpfung des Attersees. Zeitschrift für Fischerei und deren Hilfswissenschaften. Bd. XXVIII, 1930, S. 83—100. Neudamm und Berlin.
- Lechler, Hermann**, 1930, Untersuchungen über die Reinanke des Mondsees. (II.) Zeitschrift für Fischerei und deren Hilfswissenschaften. Bd. XXVIII, 1930, S. 485—493. Neudamm und Berlin.
- Mannsfeld, Wilhelm**, 1930, Studien an Coregonen des Ostbaltikums. Archiv für Hydrobiologie. Bd. XXI, Heft 1, 1930, S. 65-94. Berlin und Stuttgart.
- Monti, Rina**, 1929, Biologia dei coregoni nei laghi italiani. Rivista di Biologia. Vol. XI, Fasc. III—IV e V—VI, 1929, pp. 1—180. Milano.
- Monti, Rina**, 1930, L'ampiezza delle variazioni presentate dai coregoni italiani. Archivio Zoologico Italiano. Vol. XV, 1930, pp. 83—96. Napoli.
- Monti, Rina**, 1933, La genetica dei coregoni italiani e la loro variabilità in relazione coll'ambiente. Archivio Zoologico Italiano. Vol. XVIII, Fasc. 1—2. Napoli.
- Nüsslin, O.**, 1882, Beiträge zur Kenntnis der Coregonus-Arten des Bodensees und einiger anderer nahegelegener nordalpiner Seen. Zoologischer Anzeiger, Jahrgang 5. Leipzig.
- Oloffson, O.**, 1932, Sjöens tillväxt under en varm och en kall sommar. Ny Svensk Fiskeritidskrift, Nr. 14, 1932, S. 163—166. Göteborg.

- Otterstrøm, C. V.**, 1922, Heltling (*Coregonus albula* L.) og helt (*Coregonus lavaretus* L.) i Danmark. Undersøgelser af de Ferske Vandets Fiskeriforhold II, 1922, S. 1—50. Kolding.
- Prawdin, I. F.**, 1929, Die Suna-Maräne, *Coregonus lavaretus lavaretoides natio sunensis* nova. Bulletin of the Bureau of Applied Ichthyology. Vol. X, Fasc. 1, 1929, pp. 7—209. Leningrad.
- Pritchard, Andrew L.**, 1928, A preliminary study of the genus *Leucichthys* in the Canadian waters of Lake Ontario. University of Toronto Studies, Biological Series No. 31, Publications of the Ontario Fisheries Research Laboratory, No. 32, 1928, pp. 7—25. Toronto.
- Pritchard, Andrew L.**, 1931, Taxonomic and life history studies of the ciscoes of Lake Ontario. University of Toronto Studies, Biological Series No. 35, Publications of the Ontario Fisheries Research Laboratory, No. 41, 1931, pp. 5—78. Toronto.
- Siebold, Carl Theodor Ernst von**, 1863, Die Süßwasserfische von Mitteleuropa. 1863, S. VIII + 1—430. Leipzig.
- Surbeck, G.**, 1917, Der erste Felchen aus dem Aegerisee. Schweizerische Fischerei-Zeitung. Jahrgang 25, Nr. 4, 1917, S. 107—110. Bern.
- Surbeck, G.**, 1921, Beitrag zur Kenntnis der schweizerischen Coregonen. Schweizerische Fischerei-Zeitung. Jahrgang 29, Nr. 3, 1921, S. 52—59. Bern.
- Surbeck, G.**, 1927, Einige Bemerkungen zu E. Wagners Abhandlung über „Felchenzucht am Bodensee“. Schweizerische Fischerei-Zeitung, Jahrgang 35, Nr. 5, 1927, S. 121—123. Bern.
- Thienemann, A.**, 1912, Die Silberfelchen des Laacher Sees. Zoologische Jahrbücher, Abt. für Systematik. Bd. 32, 1912, S. 173—220. Jena.
- Thienemann, A.**, 1915, Untersuchungen an Coregonen. Zeitschrift für Fischerei und deren Hilfswissenschaften. N. F., Bd. I, 1915, S. 168—196. Berlin.
- Thienemann, A.**, 1921, Über einige schwedische Coregonen nebst Bemerkungen über die Systematik der Gattung Coregonus. Archiv für Naturgeschichte 87, Abt. A, 1921, S. 170—195. Berlin.
- Thienemann, A.**, 1928, Coregonen aus dem Ladogasee. Annales Societatis Zoolog.-Botanicae Fennicae Vanamo, Tom 6, 1928, pp. 154—161. Helsinki.
- Thienemann, A.**, 1928, Die Felchen des Laacher Sees. Zoologischer Anzeiger. Bd. LXXV, 1928, S. 226—234. Leipzig.
- Van Oosten, John**, 1929, Life history of the lake herring (*Leucichthys artedii* Le Sueur) of Lake Huron as revealed by its scales, with a critique of the scale method. Bulletin, U. S. Bureau of Fisheries. Vol. XLIV, 1928 (1929), Document No. 1053, pp. 265-428. Washington.
- Wagler, Erich**, 1927, Felchenaufzucht am Bodensee. Schweizerische Fischerei-Zeitung. Jahrgang 35, Nr. 5, 1927, S. 117—121. Bern.
- Woltereck, Richard**, 1932, Races, associations, and stratification of pelagic daphnids in some lakes of Wisconsin and other regions of the United States and Canada. Transactions of the Wisconsin Academy of Sciences, Arts and Letters. Vol. 27, 1932, pp. 487—522. Madison.

Table 1.- Description of the five lakes on whose cisco populations morphometric studies were conducted. The characteristics, color, pH, conductivity, bound CO₂, and organic matter of plankton refer to average surface conditions

Lake	Length in kilo-meters	Width in kilo-meters	Surface area (Hectares)	Maximum depth (meters)	Volume in 1000 cubic meters	Secchi disc transparency (meters)	Color, platinum cobalt scale	pH	Conductivity in reciprocal megohms	Bound CO ₂ in milligrams per litre	Organic matter of plankton in milligrams per litre
Trout (North Basin)	3.60	2.10	532	29.0	69,017	5.0	6	7.8	73	18.5	0.66
Trout (South Basin)	4.51	3.86	1,051	35.5	149,020	4.5	3	7.6	77	13.7	0.98
Mukellunge	3.30	1.18	375	19.3	26,172	4.0	4	7.3	40	10.0	1.16
Silver	1.69	0.64	87.3	19.5	9,884	5.5	4	7.5	62	15.0	0.85
Clear	2.10	1.83	373	26.5	-	6.3	0	6.6	17	2.2	0.84
Pallette✓	1.17	0.78	68.5	18.0	6,695	4.5	4	6.7	19	3.8	0.92

✓ Pallette Lake is included in this table since morphometric data on a small collection of ciscoes from this lake will be considered in an appendix.

Table 2.- Average calculated standard length in millimeters at the end of each year of life in the Trout Lake, Silver Lake, Muskellunge Lake, and Clear Lake cisco populations. Only the Clear Lake cisco shows differences in the growth (in length) of the sexes

Lake	Year of life												Total number of specimens
	1	2	3	4	5	6	7	8	9	10	11	12	
Trout	81	117	137	148	158	168	179	189	197	213	219	225	1182
Silver	80	129	155	169	181	189	196	-	-	-	-	-	564
Muskellunge	96	143	161	174	-	-	-	-	-	-	-	-	1097
Clear (male)	110	196	255	287	308	323	335	345	354	-	-	-	216
Clear (female)	109	199	260	291	312	326	340	351	361	369	376	-	224

Table 3.- Weight in grams of the different age groups of the Trout Lake, Silver Lake, Muskellunge Lake, and Clear Lake cisco populations. Except for a tendency for the Silver Lake males to be very slightly heavier than females of corresponding age, the Clear Lake cisco is the only population to show sex differences as to growth in weight

Lake	Age												Total number of specimens
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	
Trout	-	31	37	41	47	50	-	111	-	-	119	172	933
Silver	-	59	68	78	93	104	-	-	-	-	-	-	364
Muskellunge	-	46	51	60	-	-	-	-	-	-	-	-	987
Clear (male)	71	267	418	573	647	673	729	796	880	-	-	-	186
Clear (female)	80	306	530	705	770	841	917	950	1085	1062	1190	-	198

Table 4.- Age and sex of the specimens employed in the general investigation of the morphometry of the cisco in Trout Lake, Muskellunge Lake, Silver Lake, and Clear Lake

[illegible]

Table 5.— Trout Lake cisco. Value of body ratios according to age

Character	Age								
	0	II	III	IV	V	VI	VII	VIII	IX
L/H	3.90	3.91	3.86	3.86	3.83	3.81	3.71	3.84	3.87
L/D	4.98	4.25	4.24	4.30	4.28	4.25	4.08	4.10	4.17
L/W	9.73	9.25	9.18	9.22	9.42	9.21	9.11	8.44	10.90
L/AT	7.93	8.74	8.25	8.33	8.21	8.42	8.17	8.18	9.80
L/DCP	12.44	12.70	12.70	12.67	12.66	12.49	13.16	12.41	12.26
L/DB	9.52	10.52	9.76	9.71	9.81	9.56	9.60	9.67	10.08
L/AN	8.78	9.52	9.34	9.17	9.31	9.15	8.70	9.28	9.54
L/AD	13.32	14.11	14.36	14.39	14.67	14.61	14.21	14.69	15.12
L/PV	3.54	3.51	3.52	3.56	3.51	3.47	3.44	3.47	3.31
L/E	14.77	15.76	14.74	14.63	14.72	14.93	15.32	15.44	15.66
PV/AV	1.16	1.13	1.13	1.13	1.14	1.14	1.13	1.16	1.22
H/S	4.00	4.07	4.14	4.13	4.19	4.19	4.26	4.39	4.21
H/E	3.79	4.05	3.82	3.79	3.84	3.92	4.14	4.03	4.04
H/M	2.88	2.95	2.94	2.93	2.93	3.01	3.01	2.96	2.89
D/E	2.99	3.77	3.48	3.41	3.44	3.51	3.80	3.78	3.77
PV/P									
male	1.78	1.66	1.64	1.66	1.65	1.55	--	1.74	--
female		1.79	1.74	1.69	1.72	1.72	1.68	1.74	1.74
AV/V									
male	1.58	1.53	1.47	1.50	1.49	1.48	--	1.44	--
female		1.61	1.54	1.51	1.50	1.47	1.46	1.48	1.52
DE/DB	1.76	1.83	1.75	1.74	1.77	1.82	1.75	1.75	1.70
L	65	131	137	145	152	163	172	185	195
Number of specimens	17	11	44	130	56	10	4	3	2

Table 6.- Muskellunge Lake cisco, 1931. Value of body ratios according to age

Character	Age	
	II	III
L/H	4.25	4.17
L/D	4.43	4.82
L/W	3.46	9.20
L/AT	7.98	8.03
L/DCP	13.82	14.27
L/DB	9.74	9.99
L/AN	10.01	10.00
L/AD	14.02	13.89
L/PV	3.57	3.59
L/E	16.78	14.95
PV/AV	1.13	1.14
H/S	4.31	4.41
H/E	3.95	3.58
H/M	3.15	3.16
D/E	3.80	3.12
PV/P		
male	1.90	1.79
female	1.86	1.87
AV/V		
male	1.70	1.64
female	1.70	1.70
DH/DB	1.56	1.53
L	147	165
Number of specimens	29	31

Table 7.- Silver Lake cisco. Value of body ratios according to age

Character	Age						
	I	II	III	IV	V	VI	VII
L/H	4.54	4.61	4.39	4.37	4.36	4.22	4.58
L/D	4.64	4.53	4.38	4.35	4.37	4.37	4.69
L/W	9.10	8.91	8.60	8.49	8.38	8.20	8.21
L/AT	7.39	7.86	7.80	7.63	7.69	7.56	7.88
L/DCP	13.85	13.67	13.59	13.42	13.41	13.49	14.07
L/DB	9.65	9.77	9.53	9.35	9.62	9.72	8.57
L/AN	9.77	9.41	9.37	9.34	9.54	9.13	8.95
L/AD	12.84	14.11	13.50	13.54	13.55	13.61	15.15
L/PV	3.35	3.27	3.42	3.41	3.40	3.36	3.34
L/E	19.12	19.78	18.33	18.20	18.19	18.19	17.91
PV/AV	1.19	1.25	1.16	1.18	1.20	1.25	1.37
H/S	4.29	4.14	4.20	4.10	4.13	4.14	4.30
H/E	4.14	4.14	4.10	4.21	4.17	4.25	3.91
H/M	3.10	3.06	3.14	3.12	3.10	3.13	3.07
D/E	4.13	4.37	4.17	4.23	4.17	4.12	3.82
PV/P							
male	2.02	1.97	1.82	1.80	1.81	1.80	--
female	2.01	2.08	1.95	1.99	1.94	1.88	1.97
AV/V							
male	1.66	1.60	1.64	1.59	1.58	1.49	--
female	1.74	1.74	1.70	1.67	1.65	1.52	1.43
DH/DE	1.58	1.59	1.55	1.54	1.53	1.55	1.35
L	142	171	174	180	184	188	197
Number of specimens	14	7	38	67	70	13	1

Table 8.— Clear Lake cisco. Value of body ratios according to age.
Corresponding age groups of the 1931 and 1932 collections
have been combined

Character	Age									
	I	II	III	IV	V	VI	VII	VIII	IX	X
L/H										
male	4.51	4.53	4.47	4.52	4.43	4.25	4.29	4.23	--	--
female	4.54	4.57	4.64	4.54	4.58	4.32	4.48	4.35	4.48	4.45
L/D										
male	4.33	3.79	3.62	3.52	3.60	3.31	3.44	3.52	--	--
female	4.25	3.74	3.58	3.68	3.57	3.22	3.30	3.31	3.35	3.05
L/W										
male	8.64	7.27	6.81	6.48	6.39	5.44	6.08	5.86	--	--
female	8.58	6.70	6.52	6.45	5.73	5.22	5.52	5.49	5.62	6.87
L/AT	8.11	8.21	8.33	8.48	8.37	8.14	8.24	9.02	8.64	8.59
L/DCP	13.25	11.83	11.43	11.58	11.41	10.71	10.69	10.60	10.87	10.50
L/DB	8.78	8.40	8.06	8.17	8.44	7.80	8.38	8.22	8.28	7.56
L/AN	9.25	9.47	9.31	9.33	9.07	9.21	9.15	9.61	9.32	10.50
L/AD	15.49	14.30	14.20	14.40	14.25	13.28	14.02	13.95	13.99	12.60
L/PV	3.42	3.25	3.21	3.24	3.15	3.14	3.19	3.14	3.25	3.60
L/E										
male	20.03	21.27	20.83	22.09	21.06	20.80	20.49	19.09	--	--
female	20.30	21.64	21.69	22.86	22.12	20.32	21.92	20.63	23.46	19.89
PV/AV	1.11	1.14	1.14	1.14	1.15	1.16	1.12	1.18	1.07	1.02
H/S	4.42	4.45	4.57	4.46	4.38	4.47	4.41	4.80	4.36	4.47
H/E										
male	4.44	4.74	4.66	4.88	4.76	4.89	4.78	4.50	--	--
female	4.47	4.75	4.68	5.03	4.80	4.51	4.96	4.76	5.24	4.47
H/M	3.33	3.39	3.45	3.46	3.36	3.34	3.47	3.48	3.65	3.40
D/E	4.66	5.69	5.91	6.26	6.00	6.33	6.29	6.14	7.00	6.53
PV/P										
male	2.12	2.06	2.04	1.98	2.05	2.05	1.92	1.99	--	--
female	2.09	2.25	2.15	2.23	2.17	2.11	2.17	2.12	2.16	1.88
AV/V										
male	1.94	1.92	1.88	1.81	1.83	1.86	1.79	1.65	--	--
female	1.90	1.97	1.93	2.03	2.05	1.84	1.94	1.92	2.16	1.81
DH/DB	1.43	1.33	1.28	1.27	1.31	1.24	1.33	1.29	1.24	1.02
L										
male	176	247	279	306	314	315	322	334	--	--
female	176	262	300	326	342	318	352	351	364	378
Number of specimens										
male	10	15	20	6	9	5	12	1	--	--
female	10	11	20	8	4	5	10	7	2	1

Table 9.- Trout Lake cisco. Value of numerical characters according to age groups*

Character	Age								
	0	II	III	IV	V	VI	VII	VIII	IX
R	43.9	45.3	46.7	46.8	47.1	45.9	47.8	48.0	47.5
Sc	75.6	71.6	72.2	71.9	72.9	74.2	73.8	70.7	74.0
ED	7.4	7.3	7.2	7.2	7.2	7.4	7.2	7.3	7.0
EC	20.9	20.5	20.8	20.7	20.9	21.5	20.2	21.3	20.5
BR	8.1	8.1	8.5	8.5	8.5	8.6	8.8	8.0	8.5
DR	11.9	12.0	12.0	12.0	12.1	11.8	12.0	12.0	12.0
AR	12.5	12.5	12.0	12.1	12.1	11.9	11.2	11.7	11.5
PR	15.1	15.2	15.0	15.0	14.9	15.1	14.5	15.0	15.0
VR	11.8	12.0	12.0	12.0	12.0	12.0	12.2	12.3	12.0
Number of specimens	17	11	44	130	56	10	4	3	2

*To determine year class subtract age from 1931.

Table 10.- Muskellunge Lake cisco. Value of numerical characters according to age groups *

Character	Age	
	II	III
R	45.7	45.3
Sc	79.4	79.6
ED	7.5	7.6
EC	22.0	22.0
BR	8.1	8.1
DR	12.0	12.1
AR	13.0	12.9
PR	15.4	15.5
VR	12.0	11.9
Number of specimens	29	81

*To determine year class subtract age from 1931.

Table 11.- Silver Lake cisco. Value of numerical characters to age groups *

Character	Age						
	I	II	III	IV	V	VI	VII
R	45.4	45.9	45.8	45.1	44.5	45.7	41.0
Sc	78.0	79.0	76.5	78.8	78.1	80.0	82.0
RD	7.8	7.6	7.6	7.6	7.6	7.6	7.5
RC	22.1	21.4	21.5	21.4	21.6	22.2	21.0
BR	8.1	8.6	8.7	8.6	8.6	8.5	8.0
DR	12.0	11.9	12.0	12.1	11.9	12.0	13.0
AR	13.1	13.1	13.0	13.2	13.3	13.4	14.0
PR	15.9	15.9	15.7	15.5	15.6	15.6	15.0
VR	12.5	12.3	12.2	12.1	12.2	12.2	12.0
Number of specimens	14	7	38	67	70	13	1

*To determine year class subtract age from 1931.

Table 12.- Clear Lake cisco. Value of numerical characters according to year classes, 1931 and 1932 samples combined

Character	Year class									
	1931	1930	1929	1928	1927	1926	1925	1924	1923	1921
R	48.2	47.9	48.9	48.2	47.9	50.2	48.3	48.3	48.0	48.0
Sc	79.1	78.3	78.2	78.9	76.9	79.4	77.6	76.8	74.8	81.0
RD	8.5	8.5	8.5	8.5	8.5	8.5	8.5	8.5	8.5	8.5
RC	24.5	24.6	24.2	24.3	24.3	24.2	24.3	24.5	24.2	24.0
BR	9.0	8.8	8.8	8.8	8.9	8.6	8.9	8.5	8.8	9.0
DR	11.9	11.9	11.8	11.6	11.9	12.0	11.7	11.5	11.5	12.0
AR	12.9	12.6	12.4	12.2	12.5	12.4	12.4	11.9	11.8	12.0
PR	14.6	15.0	15.3	15.6	15.1	15.0	14.7	15.0	14.3	16.0
VR	12.0	11.8	11.9	12.0	12.0	12.2	12.6	12.2	12.0	12.0
Number of specimens	15	17	39	24	15	5	22	14	4	1

Table 13.- Variation of body ratios with length of fish in the Trout Lake cisco (1931)

Characters	Length interval in millimeters														
	120- 124	125- 129	130- 134	135- 139	140- 144	145- 149	150- 154	155- 159	160- 164	165- 169	170- 174	175- 179	185- 189	190- 194	195- 199
L/H	3.88	3.87	3.86	3.81	3.82	3.88	3.87	3.88	3.85	3.89	3.75	3.69	3.94	3.85	3.88
L/D	4.13	4.22	4.20	4.20	4.25	4.30	4.29	4.40	4.31	4.33	4.17	3.85	4.02	4.11	4.38
L/DCP	11.27	12.56	12.58	12.72	12.63	12.90	12.64	12.90	12.93	10.85	11.75	11.06	12.60	14.23	11.59
L/W	8.86	9.33	9.17	9.11	9.32	9.06	9.28	9.27	8.89	9.32	9.27	8.83	8.26	9.24	11.59
D/E	3.75	3.64	3.46	3.51	3.42	3.39	3.43	3.48	3.46	3.52	3.78	3.83	3.92	3.91	3.46
PV/P ♂	1.54	1.66	1.64	1.63	1.64	1.71	1.70	-	-	-	1.55	-	-	-	-
♀	-	1.76	1.68	1.70	1.70	1.71	1.70	1.71	1.73	1.75	1.70	1.79	1.69	1.80	1.82
AV/V ♂	1.60	1.50	1.45	1.45	1.49	1.51	1.54	-	-	-	1.48	-	-	-	-
♀	-	1.58	1.59	1.49	1.50	1.53	1.51	1.50	1.45	1.52	1.47	1.50	1.47	1.54	1.50
Number of specimens	1	5	8	11	20	5	9	-	-	-	1	-	-	-	-
♂	-	4	8	19	42	45	41	21	9	2	3	1	1	3	1

Table 14.- Variation of body ratios with length of fish in the Muskellunge Lake cisco (1931)

Characters	Length interval in millimeters											
	130- 134	135- 139	140- 144	145- 149	150- 154	155- 159	160- 164	165- 169	170- 174	175- 179	180- 184	
L/H	3.97	4.12	4.26	4.28	4.26	4.14	4.16	4.17	4.19	4.21	4.21	
L/D	4.37	4.00	4.26	4.45	4.47	4.62	4.70	4.83	4.87	4.83	4.78	
L/DCP	13.10	13.60	13.85	13.94	13.89	13.83	13.83	14.30	14.35	14.81	14.75	
L/W	8.19	7.56	8.18	8.60	8.27	8.35	9.03	9.13	9.48	9.60	9.32	
D/E	3.75	4.25	4.06	3.85	3.80	3.32	3.15	3.12	3.12	3.18	3.22	
PV/P ♂	-	1.81	1.90	1.87	1.97	1.75	1.76	1.81	1.82	1.80	1.76	
♀	2.00	-	-	1.89	1.92	1.71	1.85	1.85	1.90	1.94	-	
AV/V ♂	-	1.70	1.72	1.68	1.77	1.62	1.60	1.63	1.67	1.66	1.60	
♀	1.75	-	-	1.70	1.74	1.61	1.69	1.70	1.70	1.71	-	
Number of ♂ specimens	-	1	2	7	4	4	6	13	9	3	2	
♀	1	-	-	5	3	4	11	20	12	3	-	

Table 15.- Variation of body ratios with length of fish in the Silver Lake cisco (1931)

Characters	Length interval in millimeters												
	130- 134	135- 139	140- 144	145- 149	150- 154	160- 164	165- 169	170- 174	175- 179	180- 184	185- 189	190- 194	195- 199
L/E	4.32	4.59	4.59	4.50	4.43	4.36	4.37	4.36	4.35	4.35	4.41	4.39	4.50
L/D	4.96	4.75	4.52	4.46	4.84	4.44	4.42	4.31	4.35	4.35	4.37	4.47	4.69
L/DCP	13.40	13.33	13.92	13.98	14.51	14.65	13.59	13.20	13.41	13.40	13.60	13.70	13.58
L/W	8.38	9.43	9.26	8.88	8.69	9.24	8.67	8.44	8.53	8.32	8.46	8.53	8.46
D/E	3.38	3.80	4.40	4.13	4.20	4.11	4.16	4.23	4.15	4.26	4.16	4.20	3.92
PV/P ♂	2.10	2.05	1.91	1.95	2.19	2.09	1.81	1.82	1.75	1.82	1.84	1.83	1.76
♀	-	1.94	1.96	2.14	2.25	1.96	1.87	1.98	1.97	1.96	1.94	1.99	2.00
AV/V ♂	1.70	1.57	1.60	1.63	1.86	1.71	1.58	1.53	1.59	1.61	1.55	1.57	1.55
♀	-	1.66	1.83	1.64	1.70	1.58	1.64	1.66	1.70	1.65	1.66	1.60	1.65
Number of specimens	1	1	2	1	1	1	9	15	17	29	15	11	1
	-	2	4	1	1	1	5	14	24	22	19	10	3

Table 16.- Variation of body ratios with length of fish in the Clear Lake cisco (1931-1932)

Characters	Length interval in millimeters																							
	140- 149	160- 169	170- 179	180- 189	190- 199	200- 209	210- 219	230- 239	240- 249	250- 259	260- 269	270- 279	280- 289	290- 299	300- 309	310- 319	320- 329	330- 339	340- 349	350- 359	360- 369	370- 379	380- 389	
L/H ♂ ♀	- 4.53	4.49 4.46	4.68 4.56	4.46 -	- 4.56	4.44 -	4.28 -	4.38 3.97	4.58 -	4.56 4.44	4.45 4.84	4.30 4.57	4.36 4.54	4.45 4.50	4.40 4.67	4.46 4.52	4.45 4.38	4.42 4.56	4.69 4.39	- 4.46	- 4.34	- 4.48	- 4.57	
L/D ♂ ♀	- 4.46	4.54 4.52	4.64 4.31	4.06 -	- 3.99	4.19 -	3.68 -	3.72 3.39	3.64 -	3.75 3.83	3.69 3.79	3.47 3.61	3.52 3.57	3.46 3.54	3.46 3.61	3.51 3.47	3.60 3.48	3.57 3.53	3.77 3.44	- 3.39	- 3.26	- 3.28	- 3.52	
L/DCP	14.24	13.30	13.69	13.13	12.20	12.70	10.52	11.30	11.85	11.78	11.65	11.20	11.23	11.33	11.38	11.11	11.22	11.15	10.88	11.00	10.54	10.79	11.12	
L/W ♂ ♀	- 11.50	8.78 8.25	9.21 8.86	8.17 -	- 7.26	8.14 -	6.56 -	7.42 5.44	6.70 -	7.20 6.76	6.87 6.81	6.16 6.67	6.64 6.59	6.54 6.33	5.96 6.57	7.22 6.06	6.47 6.56	5.74 5.89	5.48 5.56	- 5.32	- 5.21	- 6.17	- 6.50	
D/E	4.79	4.35	4.58	4.74	5.06	4.85	5.70	5.22	5.87	5.64	5.75	5.69	6.00	6.21	6.18	6.12	5.98	6.28	6.17	6.43	6.73	6.80	6.41	
PV/P ♂ ♀	- 1.98	2.09 2.18	2.10 2.07	2.17 -	- 2.14	2.16 -	1.72 -	2.02 2.11	2.14 -	2.04 2.35	2.10 2.20	1.96 2.21	1.94 2.07	2.04 1.99	1.99 2.20	2.08 2.22	1.99 2.03	2.05 2.17	1.98 2.09	- 2.17	- 2.28	- 2.14	- 2.37	
ΔV/V ♂ ♀	- 1.76	1.97 1.87	1.91 1.90	1.90 -	- 1.95	2.02 -	1.69 -	1.96 1.81	2.04 -	1.88 2.11	1.82 1.80	1.82 1.97	1.82 1.82	1.90 1.73	1.86 1.94	1.82 1.91	1.84 2.00	1.82 1.97	1.87 1.99	- 2.01	- 1.94	- 1.90	- 1.94	
Number of ♂ specimens ♀	- 1	4 1	2 5	3 -	- 3	2 -	1 -	2 1	2 -	8 4	6 2	4 5	9 3	4 2	9 11	6 8	8 4	7 8	1 5	- 10	- 1	- 3	- 1	

Table 17.- Frequency distribution of the ratio, L/H

Interval	Lake				
	Trout	Muskellunge	Silver	Clear	
				male	female
5.20-5.29	--	--	--	1	1
5.10-5.19	--	--	--	--	--
5.00-5.09	--	--	--	--	--
4.90-4.99	--	--	--	1	2
4.80-4.89	--	--	--	1	5
4.70-4.79	--	--	8	4	8
4.60-4.69	--	--	9	12	9
4.50-4.59	--	--	35	14	20
4.40-4.49	--	5	51	16	19
4.30-4.39	--	13	37	13	6
4.20-4.29	1	39	43	7	2
4.10-4.19	4	33	23	4	3
4.00-4.09	29	17	4	3	2
3.90-3.99	69	3	--	1	1
3.80-3.89	67	--	--	--	--
3.70-3.79	61	--	--	--	--
3.60-3.69	16	--	--	--	--
3.50-3.59	12	--	--	1	--
3.40-3.49	1	--	--	--	--
Average	3.85	4.19	4.38	4.45	4.53
σ	± 0.14	± 0.11	± 0.16	± 0.24	± 0.21

Table 18.- Frequency distribution of the ratio, L/D

Interval	Lake				
	Trout	Muskellunge	Silver	Clear	
				male	female
5.60-5.79	--	1	--	--	--
5.40-5.59	--	3	--	--	--
5.20-5.39	--	4	--	--	--
5.00-5.19	--	11	5	--	--
4.80-4.99	2	23	7	1	--
4.60-4.79	11	31	36	3	--
4.40-4.59	73	20	51	1	4
4.20-4.39	79	12	62	1	2
4.00-4.19	71	5	41	9	3
3.80-3.99	20	--	8	12	10
3.60-3.79	4	--	--	20	16
3.40-3.59	--	--	--	15	19
3.20-3.39	--	--	--	9	16
3.00-3.19	--	--	--	4	6
2.80-2.99	--	--	--	3	2
Average	4.27	4.72	4.39	3.70	3.61
σ	± 0.22	± 0.32	± 0.26	± 0.40	± 0.36

Table 19.— Frequency distribution of the ratio, L/W

Interval	Lake				
	Trout	Muskellunge	Silver	Clear male	female
12.60-12.99	1	--	--	--	--
12.20-12.59	--	--	--	--	--
11.80-12.19	1	--	--	--	--
11.40-11.79	2	--	--	--	1
11.00-11.39	3	1	--	--	--
10.60-10.99	7	6	--	--	--
10.20-10.59	20	5	1	--	1
9.80-10.19	34	4	5	--	--
9.40- 9.79	36	10	13	--	--
9.00- 9.39	57	26	30	4	--
8.60- 8.99	46	17	44	3	2
8.20- 8.59	38	24	45	4	3
7.80- 8.19	13	10	48	6	3
7.40- 7.79	6	5	14	7	2
7.00- 7.39	6	2	8	8	8
6.60- 6.99	6	--	2	7	13
6.20- 6.59	--	--	--	17	11
5.80- 6.19	--	--	--	8	7
5.40- 5.79	--	--	--	7	11
5.00- 5.39	--	--	--	4	8
4.60- 4.99	--	--	--	3	4
4.20- 4.59	--	--	--	--	4
Average	9.17	8.97	8.52	6.85	6.45
σ	± 0.94	± 0.84	± 0.66	± 1.13	± 1.29

Table 20.- Relationship between (standard) length in millimeters and weight in grams in the cisco populations of Trout Lake, Muskellunge Lake, Silver Lake, and Clear Lake. Taken from Table 27 (Hile, MS.). The equations were selected on the basis of the number of specimens and the length range from which they were calculated

Lake	Year of collection	Sex	Number of specimens	Length range in millimeters	Length-weight equation
Trout	1930	♂, ♀	483	125-164	$W = 4.8834 \times 10^{-5} L^{2.71033}$
Muskellunge	1931	♂, ♀	505	130-179	$W = 141.924 \times 10^{-5} L^{2.05068}$
Silver	1930-31	♂	110	130-199	$W = 0.25532 \times 10^{-5} L^{3.32370}$
	1930-31	♀	160	135-204	$W = 0.12322 \times 10^{-5} L^{3.45372}$
Clear	1932	♂	100	160-379	$W = 0.04954 \times 10^{-5} L^{3.62476}$
	1932	♀	85	150-389	$W = 0.03652 \times 10^{-5} L^{3.68489}$

Table 21.- Frequency distribution of the ratio, L/AT

Interval	Lake			
	Trout	Muskellunge	Silver	Clear
12.00-12.49	1	--	--	--
11.50-11.99	2	--	--	--
11.00-11.49	1	--	--	--
10.50-10.99	--	--	--	1
10.00-10.49	3	--	--	1
9.50- 9.99	8	--	1	9
9.00- 9.49	22	3	2	20
8.50- 8.99	57	14	10	36
8.00- 8.49	32	42	43	50
7.50- 7.99	57	36	77	24
7.00- 7.49	24	15	61	12
6.50- 6.99	3	--	16	3
Average	8.32	8.02	7.67	8.40
σ	± 0.78	± 0.48	± 0.53	± 0.71

Table 22.- Frequency distribution of the ratio, L/DCP

Interval	Lake			
	Trout	Muskellunge	Silver	Clear
16.00-16.49	1	--	--	--
15.50-15.99	--	4	--	1
15.00-15.49	--	9	4	--
14.50-14.99	4	22	18	--
14.00-14.49	5	30	32	1
13.50-13.99	25	28	45	5
13.00-13.49	52	16	63	7
12.50-12.99	80	--	33	7
12.00-12.49	53	1	12	24
11.50-11.99	32	--	3	29
11.00-11.49	3	--	--	39
10.50-10.99	5	--	--	21
10.00-10.49	--	--	--	17
9.50- 9.99	--	--	--	2
9.00- 9.49	--	--	--	2
8.50- 8.99	--	--	--	1
Average	12.67	14.15	13.49	11.54
σ	± 0.76	± 0.68	± 0.73	± 1.02

Table 23.- Frequency distribution of the ratio, L/DB

Interval	Lake			
	Trout	Muskellunge	Silver	Clear
12.50-12.99	--	--	1	--
12.00-12.49	--	1	--	--
11.50-11.99	3	2	--	--
11.00-11.49	10	6	5	--
10.50-10.99	32	12	9	--
10.00-10.49	60	27	37	3
9.50- 9.99	65	25	55	2
9.00- 9.49	53	27	58	12
8.50- 8.99	29	7	33	36
8.00- 8.49	5	3	11	51
7.50- 7.99	1	--	1	39
7.00- 7.49	2	--	--	12
6.50- 6.99	--	--	--	1
Average	9.77	9.87	9.53	8.29
σ	± 0.76	± 0.77	± 0.71	± 0.63

Table 24.- Frequency distribution of the ratio, L/AN

Interval	Lake			
	Trout	Muskellunge	Silver	Clear
12.00-12.49	--	--	1	--
11.50-11.99	--	3	--	--
11.00-11.49	--	9	2	1
10.50-10.99	8	11	10	4
10.00-10.49	27	26	32	22
9.50- 9.99	55	37	45	31
9.00- 9.49	79	18	62	51
8.50- 8.99	60	5	49	32
8.00- 8.49	23	1	8	13
7.50- 7.99	5	--	1	2
7.00- 7.49	2	--	--	--
6.50- 6.99	1	--	--	--
Average	9.24	10.00	9.43	9.30
σ	± 0.69	± 0.70	± 0.68	± 0.61

Table 25.- Frequency distribution of the ratio, L/AD

Interval	Lake			
	Trout	Muskellunge	Silver	Clear
20.0-20.9	--	--	--	1
19.0-19.9	--	--	--	--
18.0-18.9	1	--	--	--
17.0-17.9	6	--	1	2
16.0-16.9	26	6	2	9
15.0-15.9	60	15	19	31
14.0-14.9	63	31	47	48
13.0-13.9	74	34	75	41
12.0-12.9	25	21	52	21
11.0-11.9	5	3	12	1
10.0-10.9	--	--	2	--
Average	14.4	13.9	13.5	14.3
σ	± 1.32	± 1.18	± 1.14	± 1.28

Table 26.- Frequency distribution of the ratio, L/PV

Interval	Lake			
	Trout	Muskellunge	Silver	Clear
4.10-4.19	1	2	--	--
4.00-4.09	1	--	--	--
3.90-3.99	3	1	1	--
3.80-3.89	9	9	3	2
3.70-3.79	20	17	5	3
3.60-3.69	65	23	20	3
3.50-3.59	50	25	27	9
3.40-3.49	63	18	41	20
3.30-3.39	32	10	57	17
3.20-3.29	11	5	27	27
3.10-3.19	3	--	22	30
3.00-3.09	1	--	5	25
2.90-2.99	--	--	2	12
2.80-2.89	--	--	--	8
Average	3.53	3.58	3.40	3.23
σ	± 0.16	± 0.18	± 0.18	± 0.22

Table 27.- Frequency distribution of the ratio, L/E

Interval	Lake				
	Trout	Muskellunge	Silver	Clear	
				male	female
27.0-27.9	--	--	--	1	--
26.0-26.9	--	--	--	--	--
25.0-25.9	--	--	--	--	2
24.0-24.9	--	--	--	1	2
23.0-23.9	--	--	1	3	14
22.0-22.9	--	--	4	13	11
21.0-21.9	--	--	7	21	19
20.0-21.9	--	--	14	16	14
19.0-19.9	--	1	40	14	11
18.0-18.9	2	4	64	7	4
17.0-17.9	6	8	51	1	--
16.0-16.9	28	24	23	1	1
15.0-15.9	75	28	6	--	--
14.0-14.9	93	35	--	--	--
13.0-13.9	45	9	--	--	--
12.0-12.9	9	1	--	--	--
11.0-11.9	1	--	--	--	--
10.0-10.9	1	--	--	--	--
Average	14.76	15.43	18.39	20.86	21.52
σ	± 1.16	± 1.31	± 1.46	± 1.68	± 1.74

Table 28.- Frequency distribution of the ratio, PV/AV

Interval	Lake			
	Trout	Muskellunge	Silver	Clear
1.40-1.44	--	--	1	--
1.35-1.39	1	--	4	--
1.30-1.34	4	1	13	1
1.25-1.29	15	8	23	9
1.20-1.24	26	9	53	26
1.15-1.19	59	28	59	38
1.10-1.14	73	37	24	36
1.05-1.09	54	13	22	27
1.00-1.04	24	7	5	15
0.95-0.99	2	2	1	3
0.90-0.94	2	--	--	1
Average	1.13	1.14	1.19	1.14
σ	± 0.07	± 0.07	± 0.08	± 0.08

Table 29.- Frequency distribution of the ratio, H/S

Interval	Lake			
	Trout	Muskellunge	Silver	Clear
5.40-5.59	--	--	--	1
5.20-5.39	--	--	1	4
5.00-5.19	1	3	--	3
4.80-4.99	--	5	--	19
4.60-4.79	7	10	6	24
4.40-4.59	25	39	23	43
4.20-4.39	83	27	78	38
4.00-4.19	102	20	64	17
3.80-3.99	26	4	23	6
3.60-3.79	14	2	13	1
3.40-3.59	2	--	2	--
Average	4.15	4.38	4.15	4.48
σ	± 0.23	± 0.27	± 0.24	± 0.32

Table 30.- Frequency distribution of the ratio, H/E

Interval	Lake				
	Trout	Muskellunge	Silver	Clear	
				male	female
5.80-5.99	--	--	--	1	--
5.60-5.79	--	--	--	--	1
5.40-5.59	--	--	--	--	2
5.20-5.39	--	--	1	2	7
5.00-5.19	--	--	2	7	11
4.80-4.99	1	--	3	19	12
4.60-4.79	2	--	11	16	19
4.40-4.59	4	--	31	19	16
4.20-4.39	17	5	67	14	6
4.00-4.19	64	13	49	--	2
3.80-3.99	61	13	30	--	1
3.60-3.79	71	41	16	--	--
3.40-3.59	25	22	--	--	1
3.20-3.39	13	13	--	--	--
3.00-3.19	2	2	--	--	--
2.80-2.99	--	1	--	--	--
Average	3.83	3.68	4.17	4.71	4.75
σ	± 0.29	± 0.28	± 0.29	± 0.30	± 0.35

Table 31.— Frequency distribution of the ratio, H/M

Interval	Lake			
	Trout	Muskellunge	Silver	Clear
3.90-3.99	--	--	--	1
3.80-3.89	--	--	--	3
3.70-3.79	--	--	2	8
3.60-3.69	--	--	--	14
3.50-3.59	--	3	2	25
3.40-3.49	--	5	4	34
3.30-3.39	--	14	19	30
3.20-3.29	6	17	41	24
3.10-3.19	25	20	37	11
3.00-3.09	77	41	73	6
2.90-2.99	59	7	17	--
2.80-2.89	47	3	13	--
2.70-2.79	33	--	2	--
2.60-2.69	11	--	--	--
2.50-2.59	1	--	--	--
2.40-2.49	1	--	--	--
Average	2.94	3.16	3.11	3.42
σ	± 0.15	± 0.15	± 0.16	± 0.19

Table 32.- Frequency distribution of the ratio, D/E

Interval	Lake			
	Trout	Muskellunge	Silver	Clear
8.40-8.59	--	--	--	1
8.20-8.39	--	--	--	--
8.00-8.19	--	--	--	--
7.80-7.99	--	--	--	1
7.60-7.79	--	--	--	--
7.40-7.59	--	--	--	--
7.20-7.39	--	--	--	2
7.00-7.19	--	--	--	7
6.80-6.99	--	--	--	5
6.60-6.79	--	--	--	8
6.40-6.59	--	--	--	13
6.20-6.39	--	--	--	11
6.00-6.19	--	--	--	17
5.80-5.99	--	--	--	19
5.60-5.79	--	--	--	18
5.40-5.59	--	--	--	15
5.20-5.39	--	--	2	14
5.00-5.19	--	--	4	5
4.80-4.99	--	--	2	6
4.60-4.79	1	--	18	6
4.40-4.59	1	1	32	2
4.20-4.39	3	2	57	4
4.00-4.19	13	7	48	1
3.80-3.99	14	5	19	1
3.60-3.79	50	10	22	--
3.40-3.51	73	14	4	--
3.20-3.39	59	18	2	--
3.00-3.19	40	31	--	--
2.80-2.99	5	17	--	--
2.60-2.79	1	4	--	--
2.40-2.59	--	1	--	--
Average	3.46	3.30	4.19	5.86
σ	± 0.31	± 0.40	± 0.35	± 0.76

Table 33.- Frequency distribution of the ratio, PV/P

Interval	Lake							
	Trout		Muskellunge		Silver		Clear	
	male	female	male	female	male	female	male	female
2.50-2.59	--	--	--	--	--	--	--	1
2.40-2.49	--	--	--	--	--	--	--	1
2.30-2.39	--	--	--	--	--	3	1	13
2.20-2.29	--	--	--	--	--	3	3	23
2.10-2.19	--	--	--	3	--	13	29	14
2.00-2.09	--	1	1	10	3	25	21	15
1.90-1.99	--	10	2	10	10	28	10	5
1.80-1.89	2	27	10	17	16	21	10	5
1.70-1.79	18	71	17	12	31	11	3	1
1.60-1.69	29	64	15	6	22	2	--	--
1.50-1.59	10	22	5	--	17	--	--	--
1.40-1.49	1	3	1	--	5	--	--	--
1.30-1.39	--	1	--	--	--	--	--	--
Average	1.65	1.71	1.82	1.87	1.82	1.96	2.05	2.16
σ	± 0.08	± 0.12	± 0.11	± 0.14	± 0.14	± 0.15	± 0.13	± 0.16

Table 34.- Frequency distribution of the ratio, AV/V

Interval	Lake							
	Trout		Muskellunge		Silver		Clear	
	male	female	male	female	male	female	male	female
2.30-2.39	--	--	--	--	--	--	--	1
2.20-2.29	--	--	--	--	--	--	--	--
2.10-2.19	--	--	--	--	--	1	1	7
2.00-2.09	--	--	--	1	--	--	12	19
1.90-1.99	1	--	2	1	--	2	19	27
1.80-1.89	--	--	1	4	2	9	25	15
1.70-1.79	--	7	13	22	15	34	15	7
1.60-1.69	9	31	19	22	33	33	4	--
1.50-1.59	16	78	16	7	34	16	2	1
1.40-1.49	20	59	--	1	16	10	--	1
1.30-1.39	13	22	--	--	4	1	--	--
1.20-1.29	1	2	--	--	--	--	--	--
Average	1.49	1.51	1.66	1.70	1.59	1.67	1.87	1.95
σ	± 0.12	± 0.10	± 0.10	± 0.10	± 0.11	± 0.13	± 0.12	± 0.14

Table 35.- Frequency distribution of the ratio, DH/DB

Interval	Lake			
	Trout	Muskellunge	Silver	Clear
2.10-2.19	2	--	--	--
2.00-2.09	11	--	--	--
1.90-1.99	24	--	--	--
1.80-1.89	58	3	2	--
1.70-1.79	74	4	13	--
1.60-1.69	62	26	48	5
1.50-1.59	24	40	83	7
1.40-1.49	4	24	48	15
1.30-1.39	1	11	15	54
1.20-1.29	--	2	--	52
1.10-1.19	--	--	1	21
1.00-1.09	--	--	--	2
Average	1.76	1.54	1.54	1.31
σ	± 0.14	± 0.12	± 0.11	± 0.12

Table 36.-

Frequency distribution of the number of rakers^(R) on the first branchial arch

Number of rakers	Lake			
	Trout	Muskellunge	Silver	Clear
53	--	--	--	2
52	1	--	--	7
51	6	--	1	7
50	9	--	2	20
49	20	2	7	31
48	39	5	12	44
47	86	17	34	29
46	52	32	33	11
45	31	25	43	3
44	14	19	38	1
43	14	5	13	1
42	2	5	15	--
41	1	--	11	--
40	1	--	--	--
39	1	--	1	--
Average	46.6	45.4	45.1	48.4
σ	± 1.90	± 1.48	± 2.08	± 1.70

Table 37.- Frequency distribution of the number of lateral line scales (Sc)

Number of scales	Lake			
	Trout	Muskellunge	Silver	Clear
88	1	--	--	--
87	--	--	--	--
86	--	2	5	--
85	2	--	1	1
84	--	8	7	6
83	1	5	1	4
82	--	18	11	6
81	2	20	15	16
80	4	7	34	14
79	9	11	25	16
78	11	9	27	21
77	11	9	20	21
76	12	8	23	21
75	27	5	20	12
74	21	5	8	7
73	30	2	5	6
72	32	1	2	4
71	25	--	4	1
70	34	--	1	--
69	16	--	--	--
68	16	--	1	--
67	4	--	--	--
66	11	--	--	--
65	2	--	--	--
64	1	--	--	--
63	1	--	--	--
62	2	--	--	--
61	--	--	--	--
60	1	--	--	--
Average	72.5	79.5	78.2	77.9
σ	± 3.98	± 3.07	± 3.15	± 2.94

Table 38.- Frequency distribution of the number of dorsal scale rows (RD)

Number of rows of scales	Lake			
	Trout	Muskellunge	Silver	Clear
9.5	--	--	--	2
9.0	--	--	--	1
8.5	--	9	21	153
8.0	1	1	1	--
7.5	190	100	188	--
7.0	18	--	--	--
6.5	67	--	--	--
6.0	1	--	--	--
Average	7.2	7.6	7.6	8.5
σ	± 0.44	± 0.28	± 0.30	± 0.12

Table 39.- Frequency distribution of the number of rows of scales about the caudal peduncle (RC)

Number of rows of scales	Lake			
	Trout	Muskellunge	Silver	Clear
26	--	--	1	1
25	--	--	--	54
24	--	--	--	95
23	3	--	16	6
22	49	110	81	--
21	123	--	112	--
20	98	--	--	--
19	4	--	--	--
Average	20.8	22.0	21.6	24.3
σ	± 0.77	± 0.00	± 0.70	± 0.55

Table 40.- Frequency distribution of the number of branchiostegal rays (BR)

Number of branchio- stegals	Lake			
	Trout	Muskellunge	Silver	Clear
10	1	--	5	--
9	129	15	117	130
8	130	94	86	24
7	10	1	2	2
Average	8.4	8.1	8.6	8.8
σ	± 0.57	± 0.36	± 0.55	± 0.42

Table 41.- Frequency distribution of the number of dorsal rays (DR)

Number of rays	Lake			
	Trout	Muskellunge	Silver	Clear
13	5	19	20	2
12	263	83	171	123
11	9	8	19	23
10	--	--	--	8
Average	12.0	12.1	12.0	11.8
σ	± 0.22	± 0.48	± 0.43	± 0.56

Table 42.- Frequency distribution of the number of anal rays (AR)

Number of rays	Lake			
	Trout	Muskellunge	Silver	Clear
15	--	--	2	1
14	--	10	67	18
13	54	91	117	55
12	192	9	23	56
11	31	--	1	18
10	--	--	--	6
9	--	--	--	1
8	--	--	--	1
Average	12.1	13.0	13.2	12.4
σ	± 0.55	± 0.42	± 0.66	± 1.08

Table 43.- Frequency distribution of the number of pectoral rays (PR)

Number of rays	Lake			
	Trout	Muskellunge	Silver	Clear
17	2	7	24	--
16	45	48	99	35
15	193	47	75	35
14	20	8	12	60
13	17	--	--	25
12	--	--	--	1
Average	15.0	15.5	15.6	15.1
σ	± 0.71	± 0.72	± 0.76	± 1.03

Table 44.- Frequency distribution of the number
of ventral rays (VR)

Number of rays	Lake			
	Trout	Muskellunge	Silver	Clear
14	1	--	3	--
13	16	9	45	17
12	237	81	149	116
11	23	20	13	23
Average	12.0	11.9	12.2	12.0
σ	± 0.39	± 0.50	± 0.55	± 0.50

Table 45.- Relative positions of the four populations with respect to each of the morphological characters considered, as indicated by "index numbers".

Character	Lake			
	Trout	Muskellunge	Silver	Clear
L/H	1.00	1.09	1.14	1.17
L/D	1.17	1.29	1.20	1.00
L/W	1.38	1.35	1.28	1.00
L/AT	1.08	1.05	1.00	1.10
L/DCP	1.10	1.23	1.17	1.00
L/DB	1.18	1.19	1.15	1.00
L/AN	1.00	1.08	1.02	1.01
L/AD	1.07	1.03	1.00	1.06
L/PV	1.09	1.11	1.05	1.00
L/E	1.00	1.05	1.25	1.44
PV/AV	1.00	1.01	1.05	1.01
H/S	1.00	1.06	1.00	1.08
H/E	1.04	1.00	1.13	1.28
H/M	1.00	1.07	1.06	1.16
D/E	1.05	1.00	1.27	1.78
PV/P				
male	1.00	1.10	1.10	1.24
female	1.00	1.09	1.15	1.26
AV/V				
male	1.00	1.11	1.07	1.26
female	1.00	1.13	1.11	1.29
DH/DB	1.34	1.18	1.18	1.00
R	1.03	1.01	1.00	1.07
Sc	1.00	1.10	1.08	1.07
RD	1.00	1.06	1.06	1.18
RC	1.00	1.06	1.04	1.17
BR	1.04	1.00	1.06	1.19
DR	1.03	1.03	1.03	1.00
AR	1.00	1.07	1.09	1.02
PR	1.00	1.03	1.04	1.01
VR	1.01	1.00	1.03	1.01

Table 46.- Variation of the ratio, L/H, in the Trout Lake cisco, 1931, according to length and age. The figures in parentheses show the number of specimens. Sexes combined

Length interval in millimeters	Age								Average
	II	III	IV	V	VI	VII	VIII	IX	
120-24	3.88 (1)	-	-	-	-	-	-	-	3.88 (1)
125-29	3.86 (5)	3.89 (4)	-	-	-	-	-	-	3.87 (9)
130-34	4.03 (2)	3.86 (12)	3.73 (2)	-	-	-	-	-	3.86 (16)
135-39	3.90 (3)	3.83 (11)	3.78 (16)	-	-	-	-	-	3.81 (30)
140-44	-	3.86 (12)	3.81 (43)	3.81 (7)	-	-	-	-	3.82 (62)
145-49	-	3.92 (5)	3.89 (36)	3.83 (8)	3.56 (1)	-	-	-	3.88 (50)
150-54	-	-	3.92 (27)	3.81 (21)	3.77 (2)	-	-	-	3.87 (50)
155-59	-	-	3.92 (6)	3.86 (14)	3.83 (1)	-	-	-	3.88 (21)
160-64	-	-	-	3.87 (6)	3.90 (1)	3.76 (2)	-	-	3.85 (9)
165-69	-	-	-	-	3.89 (2)	-	-	-	3.89 (2)
170-74	-	-	-	-	3.82 (3)	3.54 (1)	-	-	3.75 (4)
175-79	-	-	-	-	-	-	3.69 (1)	-	3.69 (1)
180-84	-	-	-	-	-	-	-	-	-
185-89	-	-	-	-	-	-	3.94 (1)	-	3.94 (1)
190-94	-	-	-	-	-	3.80 (1)	3.88 (1)	3.86 (1)	3.85 (3)
195-99	-	-	-	-	-	-	-	3.88 (1)	3.88 (1)
Average	3.91 (11)	3.86 (44)	3.86 (130)	3.83 (56)	3.81 (10)	3.71 (4)	3.84 (3)	3.87 (2)	(260)

Table 47.—

Variation of the ratio, L/H , in the Muskellunge Lake cisco, 1931, according to length and age. The figures in parentheses show the number of specimens. Sexes combined

Length interval in millimeters	Age		Average
	II	III	
130-34	3.97 (1)	-	3.97 (1)
135-39	4.12 (1)	-	4.12 (1)
140-44	4.26 (2)	-	4.26 (2)
145-49	4.28 (12)	-	4.28 (12)
150-54	4.26 (7)	-	4.26 (7)
155-59	4.24 (2)	4.10 (6)	4.14 (8)
160-64	4.28 (4)	4.12 (13)	4.15 (17)
165-69	-	4.19 (21)	4.19 (21)
170-74	-	4.17 (33)	4.17 (33)
175-79	-	4.28 (6)	4.28 (6)
180-84	-	4.21 (2)	4.21 (2)
Average	4.25 (29)	4.17 (81)	(110)

Table 48.— Variation of the ratio, L/H, in the Silver Lake cisco, 1931, according to length and age. The figures in parentheses show the number of specimens. Sexes combined

Length interval in millimeters	Age						Average
	I	II	III	IV	V	VI	
130-34	4.32 (1)	-	-	-	-	-	4.32 (1)
135-39	4.59 (3)	-	-	-	-	-	4.59 (3)
140-44	4.59 (6)	-	-	-	-	-	4.59 (6)
145-49	4.50 (2)	-	-	-	-	-	4.50 (2)
150-54	4.43 (2)	-	-	-	-	-	4.43 (2)
155-59	-	-	-	-	-	-	-
160-64	-	-	4.26 (1)	-	-	-	4.26 (1)
165-69	-	4.42 (1)	4.36 (4)	4.38 (2)	-	-	4.37 (7)
170-74	-	4.65 (1)	4.43 (9)	4.35 (5)	4.12 (3)	-	4.37 (18)
175-79	-	4.73 (1)	4.37 (6)	4.32 (13)	4.33 (8)	-	4.35 (28)
180-84	-	-	4.53 (3)	4.37 (19)	4.30 (13)	4.23 (1)	4.35 (36)
185-89	-	-	4.50 (2)	4.48 (9)	4.43 (9)	4.19 (4)	4.41 (24)
190-94	-	-	-	4.50 (2)	4.51 (7)	4.24 (4)	4.43 (13)
195-99	-	-	-	-	4.52 (2)	-	4.52 (2)
Average	4.54 (14)	4.60 (3)	4.42 (25)	4.38 (50)	4.37 (42)	4.22 (9)	(143)

Table 49.- Variation of the ratio, L/H, in the Clear Lake cisco, 1932, according to length and age. The figures in parentheses show the number of specimens. Sexes combined

Length interval in millimeters	Age									Average
	I	II	III	IV	V	VI	VII	VIII	IX	
140-59	4.53 (1)	-	-	-	-	-	-	-	-	4.53 (1)
160-79	4.54 (11)	-	-	-	-	-	-	-	-	4.54 (11)
180-99	4.46 (3)	-	-	-	-	-	-	-	-	4.46 (3)
200-19	-	4.44 (1)	-	-	-	-	-	-	-	4.44 (1)
220-39	-	4.48 (1)	-	-	-	-	-	-	-	4.48 (1)
240-59	-	4.65 (5)	4.13 (1)	-	-	-	-	-	-	4.56 (6)
260-79	-	4.70 (5)	4.39 (2)	-	-	-	-	-	-	4.61 (7)
280-99	-	-	4.57 (8)	-	3.96 (1)	-	-	-	-	4.50 (9)
300-19	-	-	4.76 (14)	4.45 (3)	4.57 (2)	4.26 (2)	4.26 (1)	-	-	4.63 (22)
320-39	-	-	-	4.58 (6)	4.59 (5)	-	4.39 (6)	4.23 (1)	-	4.50 (18)
340-59	-	-	-	-	4.49 (2)	-	4.49 (5)	4.29 (4)	4.47 (1)	4.42 (12)
360-79	-	-	-	-	-	-	4.50 (1)	4.34 (1)	4.48 (1)	4.44 (3)
380-99	-	-	-	-	-	-	4.57 (1)	-	-	4.57 (1)
Average	4.52 (15)	4.64 (12)	4.64 (25)	4.54 (9)	4.57 (10)	4.26 (2)	4.44 (14)	4.29 (6)	4.48 (2)	(95)

Table 50.- Comparison of the strength of the tendency for the longer fish of an age group to have the relatively shorter heads and for the older fish of a length group to have the relatively longer heads with the reverse tendencies for the longer fish of an age group to have the relatively longer heads and the older fish of a length group to have the relatively shorter heads.

Lake	Tendency for the larger fish of an age group to have the		Tendency for the older fish of a length group to have the	
	Relatively shorter heads	Relatively longer heads	Relatively longer heads	Relatively shorter heads
Trout	1.000	0.052	1.000	0.006
Muskellunge	1.000	0.381	1.000	0.000
Silver	1.000	0.159	1.000	0.021
Clear	1.000	0.104	1.000	0.052

Table 51.- Measurement of the strength of the dependence, within a population, of relative head length, eye diameter, maxillary length, body width, and fin length on rate of growth. When the tendency for the more rapidly growing individuals to have shorter heads, smaller eyes, shorter maxillaries, wider bodies, and shorter fins is set at 1.000 the quantities given in this table represent the strength of the reverse tendencies or exceptions

Lake	Tendency for the longer fish of an age group to have the relatively						
	Longer heads	Larger eyes	Longer maxillaries	Thinner bodies	Longer pectoral fins	Longer ventral fins	Longer dorsal fins
Trout	0.052	0.039	0.160	0.949	♂ 0.092 ♀ 0.336	♂ 0.301 ♀ 0.336	0.484
Muskellunge	0.381	0.124	0.424	11.012	♂ 0.202 ♀ 0.384	♂ 0.233 ♀ 0.270	0.151
Silver	0.159	0.260	1.242	0.877	♂ 0.275 ♀ 0.512	♂ 0.279 ♀ 0.928	0.371
Clear	0.104	0.189	0.576	♂ 0.299 ♀ 0.271	♂ 0.326 ♀ 0.138	♂ 0.354 ♀ 0.344	0.195
Lake	Tendency for the older fish of a size group to have the relatively						
	Shorter heads	Smaller eyes	Shorter maxillaries	Wider bodies	Shorter pectoral fins	Shorter ventral fins	Shorter dorsal fins
Trout	0.006	0.020	0.070	2.259	♂ 0.607 ♀ 0.639	♂ 0.727 ♀ 0.198	0.379
Muskellunge	Overlap of length distributions of age groups inadequate to provide a reliable comparison.						
Silver	0.021	0.137	0.608	2.986	♂ 0.258 ♀ 0.705	♂ 0.137 ♀ 0.429	0.815
Clear	0.052	0.150	0.464	♂ 8.552 ♀ 1.499	♂ 0.060 ♀ 0.352	♂ 0.049 ♀ 0.669	0.640

Table 52.- Variation according to length of seven morphometric characters in the 1928 and 1929 year classes of the Muskellunge Lake cisco, based on collections of the III-group and II-group of 1931. Below, mean value and its probable error for each character

Interval	Length distribution of the specimens		Character																										
			L/H		H/E		L/E		L/D		L/DCP		H/I		L/W														
			Y.C. 1929	Y.C. 1928	Y.C. 1929	Y.C. 1928	Y.C. 1929	Y.C. 1928	Y.C. 1929	Y.C. 1928	Y.C. 1929	Y.C. 1928	Y.C. 1929	Y.C. 1928	Y.C. 1929	Y.C. 1928	Y.C. 1929	Y.C. 1928											
130-34	1	-	3.97	-	4.12	-	16.38	-	4.37	-	13.10	-	4.10	-	8.19	-	4.10	-	8.19	-	4.10	-	8.19	-	8.19	-	8.19	-	
135-39	1	-	4.12	-	4.12	-	17.00	-	4.00	-	13.60	-	4.40	-	7.56	-	4.40	-	7.56	-	4.40	-	7.56	-	7.56	-	7.56	-	
140-44	2	-	4.26	-	4.06	-	17.31	-	4.26	-	13.85	-	3.82	-	8.18	-	3.82	-	8.18	-	3.82	-	8.18	-	8.18	-	8.18	-	
145-49	12	-	4.28	-	3.95	-	16.90	-	4.45	-	13.94	-	4.16	-	8.60	-	4.16	-	8.60	-	4.16	-	8.60	-	8.60	-	8.60	-	
150-54	7	-	4.26	-	3.95	-	16.86	-	4.47	-	13.89	-	4.05	-	8.27	-	4.05	-	8.27	-	4.05	-	8.27	-	8.27	-	8.27	-	
155-59	2	6	4.24	4.10	4.00	3.59	16.95	14.75	4.62	4.62	13.86	13.85	4.25	3.97	8.47	8.31	4.25	3.97	8.47	8.31	4.25	3.97	8.47	8.31	8.47	8.31	8.47	8.31	
160-64	4	13	4.28	4.12	3.74	3.46	16.00	14.27	4.40	4.79	13.57	13.91	3.92	3.88	8.79	9.10	3.92	3.88	8.79	9.10	3.92	3.88	8.79	9.10	8.79	9.10	8.79	9.10	
165-69	-	33	-	4.17	-	3.60	-	15.01	-	4.83	-	14.30	-	3.95	-	9.13	-	3.95	-	9.13	-	3.95	-	9.13	-	9.13	-	9.13	-
170-74	-	21	-	4.19	-	3.63	-	15.17	-	4.87	-	14.35	-	3.98	-	9.48	-	3.98	-	9.48	-	3.98	-	9.48	-	9.48	-	9.48	-
175-79	-	6	-	4.21	-	3.60	-	15.35	-	4.83	-	14.81	-	3.94	-	9.60	-	3.94	-	9.60	-	3.94	-	9.60	-	9.60	-	9.60	-
180-84	-	2	-	4.21	-	3.66	-	15.42	-	4.78	-	14.75	-	3.82	-	9.32	-	3.82	-	9.32	-	3.82	-	9.32	-	9.32	-	9.32	-
Average	150	168	4.25	4.17	3.95	3.58	16.78	14.95	4.43	4.82	13.82	14.27	4.10	3.94	8.46	9.20	4.10	3.94	8.46	9.20	4.10	3.94	8.46	9.20	8.46	9.20	8.46	9.20	
Probable error	-	-	±0.01	±0.01	±0.03	±0.02	±0.13	±0.07	±0.03	±0.02	±0.06	±0.05	±0.03	±0.01	±0.07	±0.06	±0.05	±0.03	±0.01	±0.07	±0.06	±0.03	±0.01	±0.07	±0.06	±0.07	±0.06	±0.07	±0.06

*Year class.

Table 53.- Growth histories of the four year classes appearing in the morphometric material of the Muskellunge Lake cisco, based on the 1931 collections of the 1928 and 1929 year classes and the 1932 collections of the 1930 and 1931 year classes

Year class	Year of capture	Age	Number of specimens	Length in millimeters	Calculated length in millimeters at end of year of life		
					1	2	3
1928	1931	III	81	163	99	141	166
1929	1931	II	29	150	97	138	-
1930	1932	II	24	156	100	144	-
1931	1932	I	15	139	104	-	-

Table 54.- Morphometric data for the I-group and the II-group (year classes of 1930 and 1931) of the Muskellunge Lake cisco, 1932

Year class	Age group	Number of specimens	L/H	H/E	L/E	L/D	L/DCP	H/I
1930	II	24	4.33	3.83	16.6	4.65	14.3	4.08
1931	I	15	4.39	3.89	17.1	4.61	13.5	4.05

Table 55.- Data showing the effect of the presence of the large-eyed 1928 year class in the Muskellunge Lake collection on the comparison of the relative size of the eye in the Trout Lake and Muskellunge Lake cisco populations

Lake	Year of collection	Number of specimens	Year classes	L/E	H/E
Trout	1931	260	1922 to 1929	14.8	3.83
Muskellunge	1931	110	1928 and 1929	15.4	3.68
Muskellunge	1931	81	1928	15.0	3.58
Muskellunge	1931	29	1929	16.8	3.95
Muskellunge	1932	24	1930	16.6	3.83
Muskellunge	1932	15	1931	17.1	3.89

Table 56.- Length frequency distributions (percentage frequencies in parentheses) of the 1931 and 1932 Muskellunge Lake cisco collections. The 110 preserved specimens in the 1931 collection and the 795 preserved specimens in the 1932 collection were corrected for shrinkage produced by preserving fluids before the preparation of this table

Interval in millimeters	130-34	135-39	140-44	145-49	150-54	155-59	160-64	165-69	170-74	175-79	180-84	185-89	Total
1931	7 (1.1)	9 (1.5)	51 (8.3)	93 (15.1)	62 (10.0)	44 (7.1)	131 (21.2)	129 (20.9)	73 (11.8)	15 (2.4)	3 (0.5)	-	617
1932	7 (0.7)	44 (4.5)	44 (4.5)	66 (6.7)	112 (11.4)	195 (19.9)	200 (20.4)	164 (16.7)	110 (11.2)	30 (3.1)	7 (0.7)	2 (0.2)	981

Table 57.- Comparison of the 1931 and 1932 collections of the 1928 and 1929 year classes of the Muskellunge Lake cisco with respect to relative head length, eye diameter and interorbital width

Year class	Year of capture	Age	Number of specimens	Character			
				L/H	L/E	H/E	H/I
1928	1931	III	31	4.17	14.95	3.58	3.94
	1932	IV	74	4.15	15.03	3.63	4.04
1929	1931	II	29	4.25	16.78	3.95	4.10
	1932	III	75	4.26	16.05	3.77	4.02

Table 58.— Variation with length of the ratios, L/H , L/E , H/E and H/I , in the 1932 collections of the 1928 and 1929 year classes of the Muskellunge Lake cisco. In 1932 the 1929 year class fish belonged to the III-group and the 1928 year class fish to the IV-group

Length interval in millimeters	Number of specimens		Character											
			L/H		L/E		H/E		H/I					
	Year class 1929	Year class 1928	Year class 1929	Year class 1928	Year class 1929	Year class 1928	Year class 1929	Year class 1928	Year class 1929	Year class 1928	Year class 1929	Year class 1928		
150-54	10	-	4.22	-	16.13	-	3.83	-	4.02	-	-	-		
155-59	20	4	4.22	4.15	16.09	14.63	3.81	3.53	4.16	3.95				
160-64	22	12	4.33	4.13	16.24	14.82	3.76	3.60	3.91	3.99				
165-69	14	20	4.24	4.11	15.75	14.95	3.71	3.64	4.00	4.07				
170-74	8	25	4.24	4.16	15.79	15.14	3.72	3.64	4.03	4.04				
175-79	1	9	4.44	4.22	16.29	15.26	3.67	3.62	3.85	4.02				
180-84	-	3	-	4.20	-	15.68	-	3.74	-	4.05				
185-89	-	1	-	4.11	-	14.23	-	3.46	-	4.27				
Average	162	170	4.26	4.15	16.05	15.03	3.77	3.63	4.02	4.04				
Probable error of mean			± 0.01	± 0.01	± 0.07	± 0.05	± 0.01	± 0.01	± 0.02	± 0.01	± 0.01			

Table 59.- Variation in the values of morphometric characters of the Muskellunge Lake cisco, 1932, according to length

Interval in millimeters	Number of specimens	Character					
		L/H	H/E	L/E	L/D	L/DCP	H/I
130-34	7	4.27	3.80	16.27	4.41	13.8	4.14
135-39	37	4.40	3.97	17.45	4.60	13.9	4.11
140-44	33	4.41	3.97	17.51	4.71	14.0	4.05
145-49	50	4.30	3.94	16.93	4.61	14.3	4.17
150-54	101	4.26	3.85	16.41	4.65	14.4	4.10
155-59	158	4.24	3.82	16.18	4.65	14.4	4.11
160-64	164	4.24	3.72	15.81	4.82	14.7	4.08
165-69	142	4.18	3.66	15.28	4.90	15.0	4.08
170-74	85	4.21	3.66	15.42	4.95	15.1	4.05
175-79	13	4.24	3.70	15.68	4.99	15.1	4.05
180-84	3	4.24	3.66	15.50	5.10	15.1	4.13
185-89	2	4.10	3.66	15.03	5.05	14.4	4.37
Total or mean	795	4.25	3.78	16.05	-	-	4.09

Table 60.- Frequency distribution of the number of rakers on the first arch in the V-group (1926 year class) and the III-group (1928 year class) of the 1931 Silver Lake cisco collection

Age	Number of rakers										Mean	Standard deviation	Probable error of mean
	41	42	43	44	45	46	47	48	49	50			
V	7	6	5	15	13	13	9	1	1	-	44.53	± 1.93	± 0.16
III	1	1	2	7	6	4	10	3	3	1	45.84	± 2.01	± 0.22

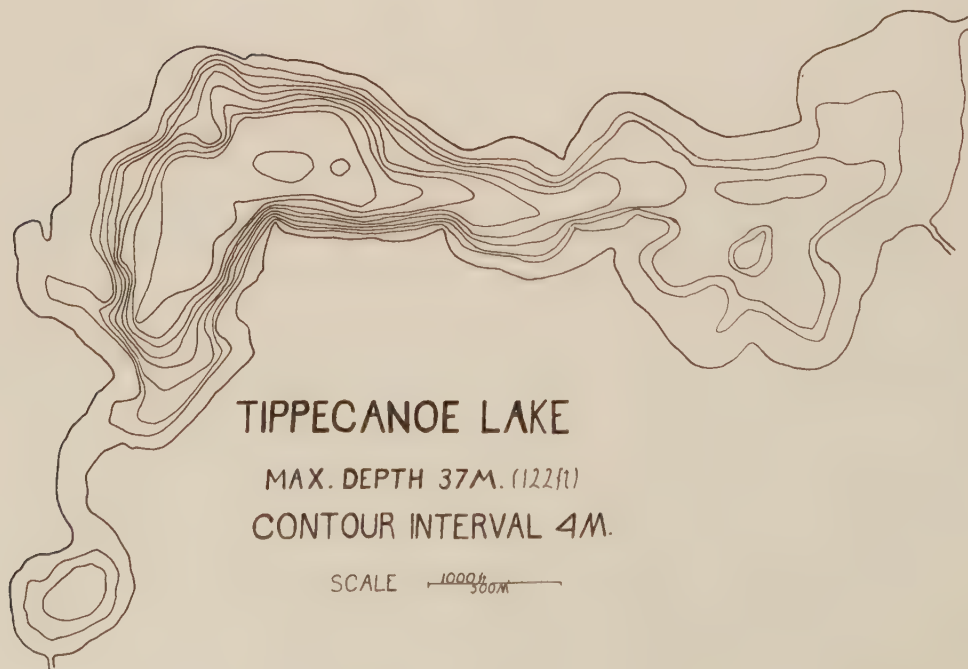
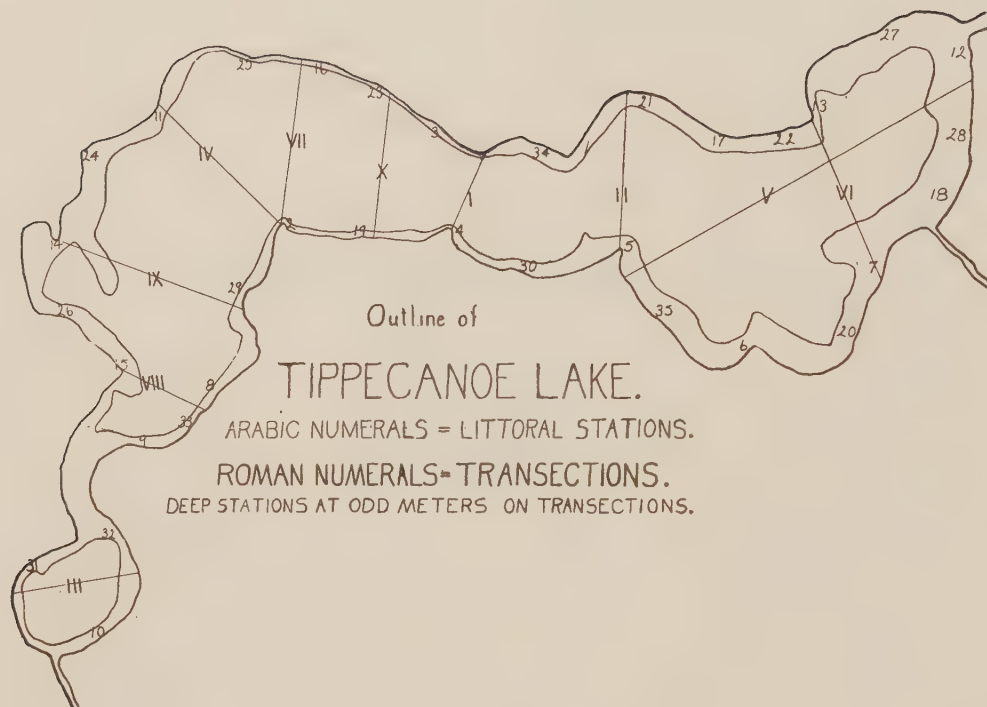
Table 61.— Tabulation of systematic characters of the subspecies of artedi recorded as occurring in Vilas and Oneida Counties, Wisconsin. Adapted from key in Koelz' (1931) publication

Subspecies	Character										Number of specimens upon which description was based
	Gill rakers	Lateral line scales	Depth (L/D)	Maxillary (H/M)	Snout (H/S)	Eye (H/E)	Pectoral fins (PV/P)	Ventral fins (AV/V)	Fin Color		
<u>atikamek</u>	u. >41 and <48	u. >70	>3.3; in fish over 225mm. u. <4; in fish under 200 mm. u. <4.5	u. 2.7-3	u. >4	-	u. >1.5 and <2.1	u. 1.4-1.6	-	8	
<u>artedi</u>	u. 46-51 but frequently fewer		u. >4	u. 2.7-3	u. 3.7-4	-	u. >1.8 in specimens over 200mm. long	-	-	-	
<u>clarensis</u>	u. 46-51 but frequently fewer	-	u. >4	u. 2.9-3.1	u. 3.9-4.2	-	u. >1.8 in specimens over 200mm. long	-	-	46	
<u>clemensi</u>	u. 46-49	u. 71-76	u. >4	2.7-2.9	3.7-4	-	u. <1.9	-	-	84	
<u>lowei</u>	u. 48-52	u. 76-78	u. >4	2.7-2.9	3.7-4	-	u. <1.9	-	-	71	
<u>wagneri</u>	(48) 52-55 (59)	u. 70 or more	u. <4	2.9-3.1	-	-	u. <1.9	-	-	9	
<u>woodi</u>	u. 47-50	u. 70 or more	u. <4	u. >2.8	-	In fish over 250mm. u. <4.5	u. 1.5-1.7	-	Not always black	15	

u. = usually

IV**THE BOTTOM FAUNA OF TIPPECANOE LAKE***by***WILL SCOTT, RALPH HILE****AND H. T. SPIETH**

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THE BOTTOM FAUNA OF TIPPECANOE LAKE.*

Will Scott, Ralph Hile and H. T. Spieth

This report is a sequel to the report on the bottom fauna of Lake Wawasee (Scott, Hile and Spieth, '28). It is a rare thing that a problem is of such a type and conditions are such that an experiment can be undertaken which will involve an entire lake. Occasionally such a situation arises. The work of Woltereck ('31) on the transplantation of Cladocera to the Italian Lakes is a good example. Usually it is only by investigating phenomena in different lakes where different conditions prevail that significant factors finally become apparent.

Wawasee and Tippecanoe Lakes are near each other, approximately five miles (eight kilometers) apart. They lie in different drainage systems. Wawasee is in the St. Lawrence system, while Tippecanoe is tributary to the Mississippi. Wawasee is the largest lake in the state, while Tippecanoe is the deepest. Other differences will be noted under morphometry and the distribution of temperature and gases.

LOCATION

Tippecanoe Lake is located in Kosciusko County, Indiana. It occupies parts of sections 1, 11, and 12 of T 33 N, R 6 E; and parts of sections 7, 8, 9, 16, 17, and 18 of T 33 N, and R 7 E. It is approximately Lat. $40^{\circ} 27' N$, and Long. $88^{\circ} 46' W$. The lake is less than two miles south of the continental divide, which separates the St. Lawrence and Mississippi River systems. It lies in the massive Huron-Erie, Saginaw interlobate moraine. Its formation has already been discussed (Scott '16 p. 5 and '31 p. 65) and need not be repeated, except to say that additional field observations have not changed this original generalization.

The Tippecanoe River forms the outlet of this lake. The two tributaries of the lake are each called Grassy Creek. The one from the east brings water from Webster, Backwater, Smalley, and Crooked Lakes. The one from the southeast drains the Barbee Lake system, Ridinger Lake, and Robinson Lake.

The field work was done by Drs. Hile and Spieth under the supervision of the senior author. The general plan of taking collections formulated for the work on Wawasee was used on Tippecanoe. At each littoral station collections were made at depths of .25 meter, .75 meter, 1.00 meter and 1.25 meter. The collections at each depth were counted separately. For these collections the hoe dredge was used. Beginning at three meters, collections with an Ekman dredge were made at odd meter depths on definite transection lines. These lines are indicated on the map. On them were made 176 deep water collections. There were 35 littoral stations and 140 littoral collections.

FORM OF THE LAKE

The Lake is sigmoid in form with its longer dimension approximately east and west. It is divided into three basins which are designated as the east basin, the middle basin, and Oswego basin. The separation of the east and middle basins is not very distinct. The point where the south shore turns from northwest to west (known locally as Government Point) is taken as the point of

* Contribution No. 254 from the Zoological Laboratory of Indiana University.

separation of these two basins. The Oswego basin is much more distinct and is separated from the middle basin by a channel 400 ft. (120 m.) wide and about 13 ft. (4 m.) deep.

In former times what is now called James Lake (not to be confused with a lake of the same name in Steuben County) was a part of Tippecanoe Lake. Now, however, it is separated from Tippecanoe Lake by a marsh of considerable area and connected with it by a narrow meandering channel, so that it is physically and biologically distinct.

MORPHOMETRY

The morphometry is indicated in Table I, which compares Tippecanoe Lake with Wawasee. While the area of Wawasee is 3.7 times that of Tippecanoe, its volume is only 2.2 times that of the latter. This relationship is shown also by the greater average depth of Tippecanoe Lake. Tippecanoe has an average slope of 7.2 which is more than twice that of Wawasee. The steepest average slope in Wawasee occurs between 4 meters and 8 meters, while that of Tippecanoe is 20 meters deeper.

TABLE I. COMPARING THE MORPHOMETRY OF.

	Wawasee Lake	Tippecanoe Lake
Area.....	11,608,768 sq. M. (2,867 acres)	3,091,920 sq. M. (963 acres)
Volume.....	77,770,751 cu. M.	34,865,278 cu. M.
Average Depth.....	6.69 M. 21.94 ft.	11.28 M. 36.99 ft.
Maximum Depth.....	23 M. 75 ft.	37.1 M. 122 ft.
Average Slope (total).....	3.47	7.2
Length of shore line.....	25,325 M. 15.7 miles	13,112 M. 8.1 miles
Shore Development.....	2.0	2.1
Volume Development.....	87.2%	88.1%
% area S-4.....	51.9	38.4
Slope S-4.....	1.8	4.2
Length Mid Channel.....	7,713 M. 4.79 Miles	5,182 M. 3.2 Miles
Width Average Area	1,519 M.	596 M.
Length	.94 Miles	.37 Miles

The steepest slope in Tippecanoe Lake occurs off Silver Point, where from the shore to a depth of 32 meters (104 ft.) the slope is 32.8%. While this is not as steep as the submerged "cliffs" that form a part of the bottom of Green Lake and Devils Lake in Wisconsin (Juday '14), or Canyon Lake in the Huron Mountains of Michigan (Scott, '21), or in any of the "crater" lakes, it is a remarkably steep slope for a lake bottom composed entirely of glacial drift. In shore development and bottom development the two lakes are almost identical. So far as is known, Tippecanoe is the deepest lake in Indiana.

ECOLOGIC CHARACTERISTICS OF THE BASINS

The Middle Basin

The middle basin is characterized by steep slopes. The littoral has little or no vegetation except in two embayments; one to the northwest and a second on the south to the west of "Silver Point." Along most of the shoreline there is a narrow "cut and fill" terrace from which surrounding moraines rise abruptly on one side and the water deepens rapidly on the other. These shores, especially those with a N.W.-S.E. direction are exposed to erosion by waves and currents. During the summer stratification, this movement is limited to the epilimnion which in this lake extends to a depth of six meters. Eggleton ('31) has shown that during the vernal and autumnal overturn, currents of sufficient velocity to move organic material extend to the deeper levels of a lake.

The steep slopes and the erosive action of waves and currents have resulted in a clean gravel bottom over much of this part of the littoral. Off "Silver Point," where this slope is at a maximum, this gravel bottom extends to a depth of twenty meters.

The East Basin

This basin is one of gentle slope. It is bordered by marshes especially on the east and south. There is a dense growth of submerged aquatic plants near the entrance of a ditch on the northwest and a larger but much less dense area of Potamogeton where the effluent from the east empties. There is a scattered growth of Scirpus off "Government Point" and on the shoal to the east of this point.

However, most of the bottom of the shallower part of this basin is covered with marl-forming algae and its product. On this marl occur both Potamogeton and Chara, but the plants are stunted and scattered.

The Oswego Basin

This basin is the smallest of the three. It is at the west end of the lake and is surrounded by moranic deposits which reach an elevation of 30 to 50 ft. (10-15 meters) above the lake. These two conditions protect it from wave action. The northwest side of this basin and both sides of the channel which connect it with the middle basin are bordered by marsh with a maximum width exceeding 300 ft. (100 meters).

In the shallow water of the littoral grow not only rushes (Scirpus), Pontederia, Sagittaria, yellow water lily (Nymphaea) and the white water lily (Castelia), but also the swamp loosestrife (Decodon). This latter fills small

lakes rapidly by its peculiar habit of forming roots at the tip of any branch that touches the water. They also develop air cells in the epidermis near the water line, thus forming a float for the plant. The channel and the deeper littoral of this basin contain dense growths of *Myriophyllum*, *Ceratophyllum*, and several species of *Potamogeton*. Where these are absent the bottom is covered with *Chara*. On the bottom of the deeper part of this basin is a thick deposit of organic material derived chiefly from these plants of the littoral.

THE THREE BASINS COMPARED

The three basins not only exhibit different stages in development but the East basin and the Oswego basin exhibit divergence.

The middle basin is nearer the original, oligotropic condition than the other two. It is deep; its shores are composed largely of glacial gravel which extends to considerable but varying depths. Organic deposits cover a much more limited part of its bottom area.

The East basin, as already indicated, is dominated by marl-forming algae, while the Oswego basin is similarly dominated by aquatic phanerogams. How this tendency toward marl on one end and peat on the other originated, is not apparent. Each tendency, however, seems to be cumulative and limiting. The conditions in these two basins are not unique. The third basin of James Lake (Steuben County) and Wabekan Lake of Wisconsin are similar to the East basin. Heriff Lake in Noble County is nearing the end point brought about by the processes at work in Oswego basin.

The midsummer distribution of temperature and oxygen is very different in the Middle and Oswego basins.

Due to the smaller size of the Oswego basin and the protection from wind it receives from the surrounding moraines, it becomes stratified slightly earlier. Its thermocline lies between four and eight meters. In the middle basin the thermocline in early August usually lies between seven and twelve meters. The oxygen always disappears from the lower levels of the Oswego basin by midsummer. Some oxygen always remains below 32 meters in the middle basin.

However, by August the middle basin develops a thermocline "oxygen notch." At about ten meters the oxygen is very much reduced and possibly entirely disappears just before the thermocline begins to descend. The complete disappearance of the oxygen at this level has not been observed. This phenomenon is associated with a relatively large production of plankton.

To describe these two basins in developmental terms, the middle basin is oligotropic approaching eutropic condition, while the Oswego basin is beyond the typical eutropic and approaching the dysentropic stage. The oxygen and temperature conditions in the middle basin form a favorable physical habitat for the Cisco (*Argyrosomus arctedi cisco*, Jordan) which are present in large numbers.

DISTRIBUTION OF THE LITTORAL FORMS

DEPTH

As stated above, the collections at all littoral stations were made at four depths: .25 M., .75 M., 1 M., and 1.25 M. Some of the forms were rather gen-

erally distributed over all these depths while other groups showed a very definite maximum.

Among the crustacea, the amphipods are rather evenly distributed, varying only from 730 per square meter at .25 M. to 981 at .100 M. and 736 at 1.25 M. The Isopoda, however, show a very definite maximum at .25 M. The numbers in order are 56.8, 5.14, 3.14, and 9.14 per square meter. The Gastropoda are fairly evenly distributed with the exception of two genera, Goniobasis and Planorbis. The former has its maximum at .25 and the latter at 1.00 M. Goniobasis is eight times as numerous at this depth as at any of the other three, while the ratio for Planorbis is nearly four. The details are exhibited in Table II.

Of the insects the Chironomidae alone gradually increase with the depth. The Ephemeridae are rather more numerous at 1.00. Sialis shows a marked maximum at .75.

TABLE II. DISTRIBUTION OF LITTORAL FORMS

	Average per Sq. M.					Max. per Sq. M.	Station Max.	Depth Max.	Max. Av.
	.5 M.	.75 M.	1.00 M.	1.25 M.	Total Littoral				
Platyhelminthes									
Turbellaria.....	5.71	12.8	26.8	7.42	13.18	580	11	1.00	43
Annelida									
Oligochaeta.....	72	34	33	11	37.5	1,410	16	.25	37
Hirudinea.....	4	4.85	4.28	.85	3.49	80	12	.75	22
Mollusca									
Pisidium.....	1.42	.57	2	.57	1.14	40	12	1	35
Goniobasis.....	37.1	4.28	2.85	.85	11.27	110	8	.75	9
Planorbis.....	2.85	12.85	48.85	8.56	18.27	1,390	11	1	76
Physa.....	32	31.4	58.2	37.1	49.67	1,440	9	.25	28
Amnicola.....	39.4	52	49.1	30.2	42.65	480	2	.75	11
Valvata.....	2	2.2	.85	2	1.78	50	32	.75	28
Lymnea.....	.57	.85	0	.28	.42	20	10	.75	47
Cameloma.....	2.58	1.71	1.42	.28	1.49	50	11	1	33
Arthropoda									
Crustacea									
Camburus.....	.57	2.57	1.14	1.71	1.49	90	35	.75	60
Amphipoda.....	730	806	981	726	809.5	9,610	11	1	11
Isopoda.....	56.8	5.14	3.14	9.14	18.55	1,870	2	.25	100
Insecta									
Odonata									
Zygoptera.....	7.7	11.5	8.5	10	9.42	180	2	.75	19
Anisoptera.....	.57	2.57	1.42	2	1.64	60	32	.75	36
Diptera									
Chironomidae.....	313	320	400	418	362.74	2,810	25	.25	7.9
Other diptera.....	19.4	10.2	16.5	10.5	14.15	190	22	.25	13
Ephemeridae.....	33.7	33.7	47.1	32	36.62	310	9	1.25	8.4
Megaloptera									
Sialis.....	1.57	20.57	6.85	4	8.99	160	19	.75	17
Hydrocarina.....	32.2	56.2	57.7	52.2	49.57	280	29	1	5.6

The Oligochaetes are more numerous at .25 and gradually decrease as the depth increases so far as the littoral is concerned. The leeches, on the other hand, show a decided preference for the intermediate depths of .75 and 1.00 M. The Turbellaria have approximately the same distribution as the Hirudinea.

REGULARITY OF DISTRIBUTION IN THE LITTORAL

Because of a marked preference for some particular habitat, a bit of debris, a clump of plants, or some other set of factors, some littoral forms are numerous at one station and sparse at another. Other forms are distributed more generally. This may be indicated as a ratio, obtained by dividing the maximum number at any station by the average number for the whole littoral. The Isopods, for instance, are strikingly local due to their preference for decaying organic material, while the Hydrocarina, which rove generally over the bottom, are more evenly distributed. The factor for the former in this lake is 101, while that of the latter is 5.2.

The more generally distributed forms and their factors are Hydrocarina 5.2, Chironomidae 7.7, Ephemerida 8.7, Tricoptera 9, Amphipoda 11, other Diptera 13, Amnicola 16, Sialis 17, Zygoptera 18. The more limited the category, the more significant are the ratios. Sialis includes single species in the lake, while the Hydrocarina includes several. See Table II.

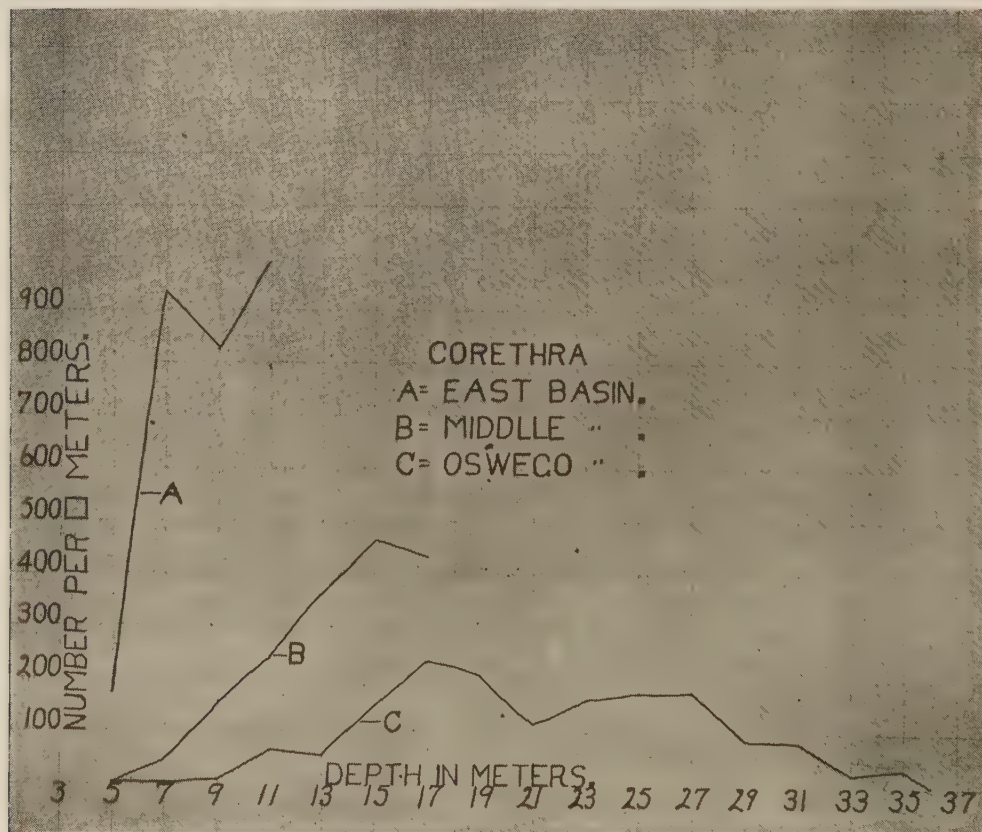


FIGURE I

DEEP WATER FAUNA

The deep water fauna, that is, the fauna of three meters and beyond, in Tippecanoe Lake consists of two elements. The first is the littoral forms that range for varying distances into the deep water. This is indicated in tables.

The second is composed of strictly benthic forms, which in this lake are chironomid larvae, *Corethra* larvae and tubificid worms. The Sphaeriidae, which are so common in many of the nearby lakes, occur very sparsely in Tippecanoe. The distribution of these dominant deep water forms is as follows:

Corethra (Chaoborus)

The curves for *Corethra* are significantly different in the three basins. At all depths they are much more numerous in the Oswego basin than in the other two. At the deeper stations (7, 9, and 11 meters) in the Oswego basin the population exceeds 800 per square meter. The maximum for the whole lake, 990 per square meter, occurs at 11 meters in this basin.

The population at each of these depths is less in the middle basin. The maximum for the middle basin (234 per square meter) is at a depth of 15 meters. From 27 meters to 35 meters the number decreases. None was found at 37 meters.

The curve for the east basin has the same general form as that for the middle basin, but the population at each level beyond 5 meters is greater than it is at a corresponding level in the middle basin.

The difference in distribution in the three basins may be explained by correlating what is known of the habits of *Corethra* in general and the distribution

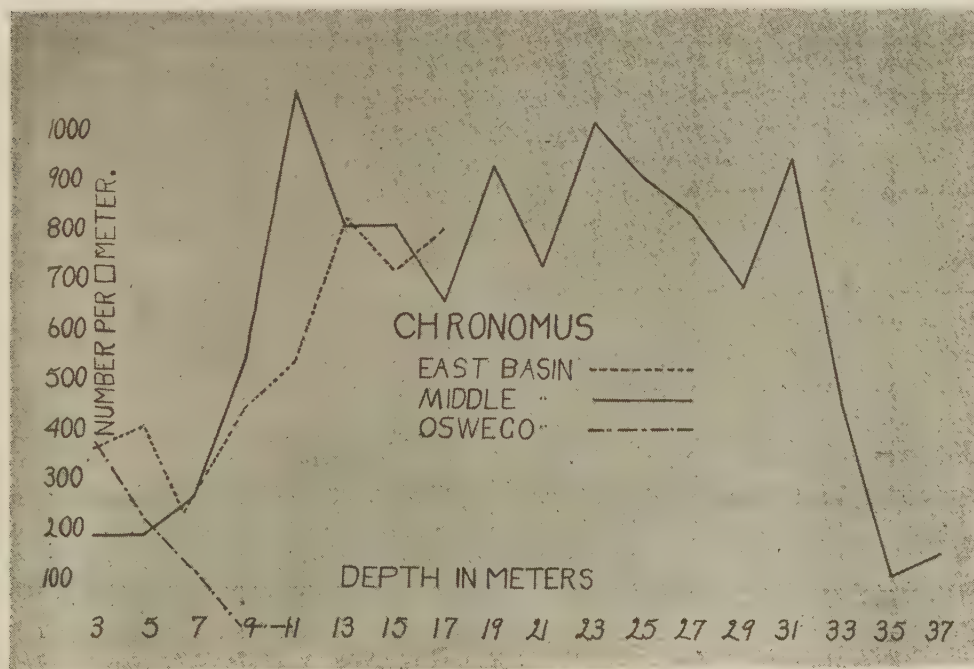


FIGURE II

of the Cisco (*Argyrosomus artemi cisco*, Jordan) in Tippecanoe Lake. The genus *Corethra* is not tied to the bottom as are the larvae of the chironomids. In some lakes *Corethra* is always an element of the plankton. Juday '21 has shown that in Lake Mendota these larvae that are one-third grown or larger, spend the day in the mud at the bottom and shortly after sunset migrate to, or at least toward, the surface, returning to the bottom next morning.

The middle basin of Tippecanoe Lake, and to a limited extent the east basin, has a large Cisco population. During the breeding run in 1933, seven thousand pounds of Cisco were netted. In the summer when the lake is thermally stratified, they are confined to the hypolimnion and the lower part of the thermocline. As has been pointed out, the east basin at its lower levels is similar to and continuous with the middle basin. However, more than ninety-five per cent of the hypolimnion of the two lies in the middle basin.

So far as is known, there are no Cisco in the Oswego basin. During the summer stagnation, there are few in the east basin. A much larger number is present in the middle basin. The Cisco feed on the diurnally migrating *Corethra*, thus making the number of *Corethra* in the three basins inversely proportional to the number of Cisco.

Chironomidae

The distribution of the Chironomidae in the Oswego basin appears to be quite different from the distribution of these larvae in the east and middle

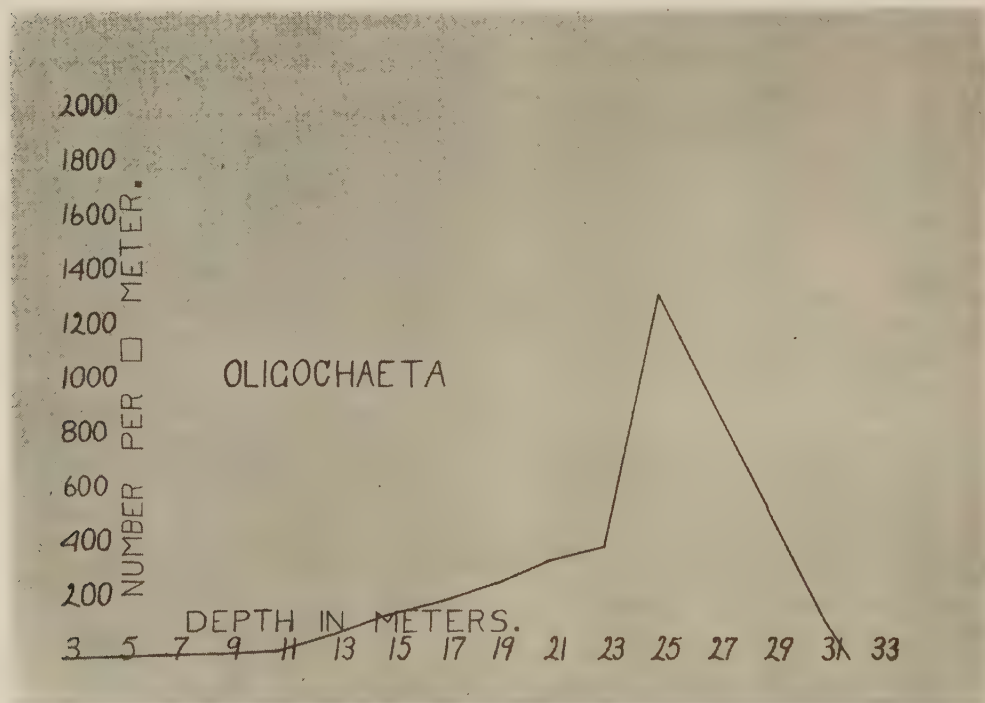


FIGURE III

basins. Although the form of the curve is different, the underlying cause of this distribution is the same in both instances.

In the Oswego basin the number of Chironomids at three meters is 495. The population decreases regularly and rapidly with the depth until at nine meters there are only 29 per square meter.

In the middle basin the maximum is reached at 11 meters where there are 1,094 per square meter. For the next twenty meters the number remains high, varying between the above maximum and 706. At 31 meters the population is 968 per square meter. From this point the number per square meter declines rapidly until at 35 meters there were only 139. The curve for the east basin approximates that of the middle basin.

The unfavorable conditions which are present in the deeper levels of the middle basin are found at much higher levels in the Oswego basin and are associated with the decline of the Chironomid population beyond the depth of three meters.

Oligochaeta

There were few oligochaets from 3 to 13 meters. In this area they averaged less than 50 per square meter. For the next ten meters the number gradually rose until at 23 meters the average was 415. From 23 to 27 meters the number increased rapidly to a maximum average of 2,225 per square meter. From 27 to 31 the population declined rapidly. At 31 meters there were only 31, and at the deeper stations none was taken.

Discussion of the deep water benthic fauna

In the middle basin the curve for both the oligochaets and the Chironomidae show what Eggleton '31 has called a "concentration zone." A similar curve for at least certain bottom organisms has been found in Lake Simcoe (Rawson '28) Turkey Lake (Scott, Hile, and Spieth '28), several of the Holstein Lakes in Germany (Lundbeck '26), and others.

The causes of this midsummer distribution are probably diverse and complex. We have these suggestions to offer. In the deeper waters of the middle basin in Tippecanoe Lake the bottom is overlaid with a flocculent deposit of organic material. Its texture is such that a sounding lead will sink at least two meters deeper than the level from which clear water can be pumped. This unstable substratum probably forms an unfavorable condition for such tubiculous forms as the oligochaets and the Chironomidae. The oxygen just above the substratum is always reduced during the summer stagnation. While it rarely, if ever, reaches a condition where the effect is lethal, it certainly is considerably below the optimum.

The decrease in numbers nearer the shore is related to higher temperature and increased rate of metabolism. In an attempt to test this hypothesis, a set of traps designed to capture emerging insects was set over different depths on Winona Lake. While the detailed data are reserved for a later communication, it may be stated that at five meters there were 1,281 larvae on June 14, 1934, and on August 27 there were 756 per square meter and that during this period there had emerged 8,668 insects. Below the thermocline at eleven meters these

numbers were respectively 3,927, 4,221, and 2,536. That is, in the epilimnion there had emerged between these two dates 645% as many insects as there were larvae at the beginning of the period, while below the thermocline the per cent was 64. It seems possible that in the epilimnion the higher temperature with the consequent increased rate of metabolism speeds up the life cycle so that with a relatively sparser population at any one time, a greater number of imagoes is produced.

In the lower part of the thermocline and the upper part of the hypolimnion there is neither the unfavorable condition which is found on the bottom at the point of maximum depth nor the high metabolic rate of the epilimnion, with the result that a more numerous bottom population is maintained during this season.

The conditions in the upper hypolimnion and the epilimnion respectively seem to be analagous to that found in plankton of the ocean, in the arctic, and in the tropics. In the arctic the rate of metabolism is low and the population dense, while in low latitudes the rate of metabolism is high and the population relatively sparse.

Comparison of Tippecanoe Lake and Lake Wawasee

When the deep water bottom fauna of these two lakes is compared gravimetrically (see Table III), the amount present in Lake Wawasee is a trifle more than four times the average amount found in Tippecanoe. The littoral of Wawasee produces 3.7 times that of Tippecanoe. See Table IV.

If the general characteristics of the two lakes are compared in order to determine whether or not there may be some physical difference correlated with this difference in benthic productivity, the following is the result.

Their difference in latitude is only five miles (eight kilometers). Their basins are in the same sort of glacial drift. The lakes do not differ significantly

TABLE III

	Lake Tippecanoe		Lake Wawasee	
	Lbs. Per Acre	Kilos Per Hectare	Lbs. Per Acre	Kilos Per Hectare
Oligochaeta.....	4.19	4.49	4.6	5
Chironomidae.....	58.7	66.0	332.62	365.88
Corethra.....	1.8	2.0	3.06	3.36
Sialis.....	19.4	21.8	12.34	13.57
Total.....	84.09	94.29	352.62	387.81

Comparison of wet weights of the principal bottom forms below the three meter contour in Tippecanoe Lake and Wawasee Lake. The weight of these forms per unit area in Wawasee is 4.19 times the amount in Tippecanoe.

TABLE IV

	Grams	Lbs.	Lbs. Per A.
Turbellaria.....	24,434	53	.36
Oligochaeta.....	151,744	334	2.31
Pisidium.....	21,963	48	.33
Goniobasis.....	1,631,419	3,571	24.79
Planorbis.....	779,664	1,717	11.92
Physa.....	1,678,224	3,696	25.66
Amnicola.....	379,461	835	5.79
Valvata.....	563,045	1,240	8.54
Cambarus.....	625,769	1,378	9.56
Amphiopoda.....	1,450,762	3,270	22.70
Isopoda.....	40,094	88	.61
Chironomidae.....	1,418,449	3,129	21.70
Ephemeraidae.....	88,863	195	1.35
Sialis.....	69,942	154	1.06
	8,913,833 or 8,913 Kilos	19,704	136.68 or 153 Kilos per Hectare

The littoral benthic fauna of Tippecanoe Lake expressed as totals and pounds per A. The amount of the littoral bottom fauna of Wawasee is about 3.75 times that of Tippecanoe.

in size. Wawasee is the larger, but the wave action on the two is approximately equal.

The shore development of Lake Wawasee is 2.0, while that of Tippecanoe is 2.1. The volume development of the two lakes is 87.2 and 88.1 respectively.

The only physical characteristics in which the two lakes differ markedly is in slope. The average slope of Wawasee is 3.7, while that of Tippecanoe is 7.2. It seems evident that slope may have some significance as an indicator of lake productivity, at least of benthic productivity.

Klug ('26) has suggested that the amount of plants (phanerogams) growing in a lake is the most reliable index to its productivity. Rawson (l. c.) uses the data from seven lakes to show that in lakes of less than 40 square miles area and a depth of 100 feet or less, or in larger or deeper lakes if the excess of the above limits be ignored, the fauna would vary inversely with the product of the depth in feet and the area in square miles. Pearsall ('20) found that the number and kind of rooted aquatic plants depend upon the nature of the sediment on which they grew.

All of these factors are intimately related to slope. In a lake of a given size, slope determines the relation of the littoral to that of the deep water. In lakes of the same slope but of different size, the per cent of the littoral is related to the area.

Granting that the aquatic phanerogams are the major source of the organic material which serves as food for the benthic forms, it appears that the productivity of a lake bottom would vary indirectly with the slope and the size of the

lake. So far as the two lakes discussed in this paper are concerned, slope is the more important of these two factors.

This suggestion could not apply to lakes of such a size and exposure, that the wave action would entirely prevent the development of aquatic phanogams. In such lakes the phytoplankton must be the only source of carbohydrates.

The senior author is wholly responsible for the suggestions and conclusions in this paper.

LITERATURE CITED

EGGLETON, FRANK E.

1931. A limnological study of the profundal bottom fauna of certain fresh water lakes. Ecol. Monog. 1, 3:231-331.

JUDAY, C.

1914. The inland lakes of Wisconsin. The hydrography and morphometry of the lakes. Wis. Geol. and Nat. Hist. Sur. Bull. XXVII, Sci. Ser. :1-137.

KLUG, A. BROOKER.

1926. The productivity of lakes. Quart. Rev. Biol. 1:572-577.

LUNDBECK, J.

1926. Die Bodentierwelt der Norddeutscher Seen. Archiv. f. Hydrobiol. Suppl. 7:1-437.

PEARSALL, W. H.

1920. The aquatic vegetation of the English lakes. Jour. Ecol. 8:163-199.

RAWSON, D. S.

1930. The bottom fauna of Lake Simcoe and its role in the ecology of the lake. Univ. Toronto Studies. Pub. Ont. Fish. Res. Lab. No. 40.

SCOTT, I. D.

1921. Inland lakes of Michigan. Mich. Geol. and Biol. Surv. Pub. 30. Geol. Ser. 25:1-383.

SCOTT, WILL; RALPH HILE, and H. T. SPIETH.

- Investigation of Indiana Lakes. A quantitative study of the bottom fauna of lake Wawasee (Turkey). Dept. Cons. Ind. Pub. Div. Fish. and Game. 1:1-25.

WOLTERECK, R.

1928. Über die Population Frederiksborger Schloss-See von *Daphnia cuculata* und einige daraus neuentstandene Erbrassen besonders diejenige des Nemi-Sees. Int. Rev. d. ges. Hydrobiol. u. Hydrograph. 19:172-203.

AGE AND GROWTH OF THE ROCK BASS,
AMBLOPLITES RUPESTRIS (RAFINESQUE),
IN NEBISH LAKE, WISCONSIN¹

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INTRODUCTION

The present study of the age and growth of the Nebish Lake rock bass is another in a series of papers that have been based wholly or in part on materials collected in the course of investigations on the fishes of the lakes of the northeastern highlands, Wisconsin, conducted cooperatively by the Wisconsin Geological and Natural History Survey and the United States Bureau of Fisheries over the periods, 1927-1928 and 1930-1932. The publications have included studies of the age and growth of the rock bass (Wright, 1929), whitefish (Hile and Deason, 1934), yellow perch (Schneberger, 1935), cisco (Hile, 1936a), muskellunge (Schloemer, 1936, 1938), largemouth black bass (Bennett, 1937), common sucker (Speer, 1938), and smallmouth black bass (Bennett, 1938). A total of five mimeographed reports on the growth of game fish in Wisconsin has been issued by Juday and Schneberger (1930, 1933), Juday and Bennett (1935), and Juday and Schloemer (1936, 1938). In addition there have appeared two publications on the morphometry of the cisco (Hile 1936b, 1937), three dealing with the parasites of fishes in the region (Cross 1934, 1935, 1938) and one on the food of fishes (Couey, 1935). A paper by Hile and Juday on the bathymetric distribution of fish will appear simultaneously with the present study of the rock bass. A contribution on the growth of the bluegill by Schloemer will be published in the near future.

The rock bass, *Ambloplites rupestris* (Rafinesque), occurs from "North Dakota to the southern parts of Ontario and Quebec, southward to Oklahoma, Arkansas and northern Alabama,

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and in the Atlantic drainage south to the Susquehanna in New York" (Greene, 1935). Earlier, the rock bass was reported from Louisiana and Texas (Jordan and Evermann, 1896). However, the southern rock bass was described as a new species, *Ambloplites ariommus*, by Viosca (1936). This form is probably typical of the Gulf coastal area.

The northern rock bass, *A. rupestris*, occurs abundantly both as a lake and as a stream fish. Forbes and Richardson (1920) stated that in Illinois the rock bass exhibits a "decided preference for clear rocky, streams" and for "swift water." (They emphasized the close association of the rock bass and the small-mouth black bass.) In Wisconsin, on the other hand, the rock bass appears to be characteristic of lakes rather than streams.

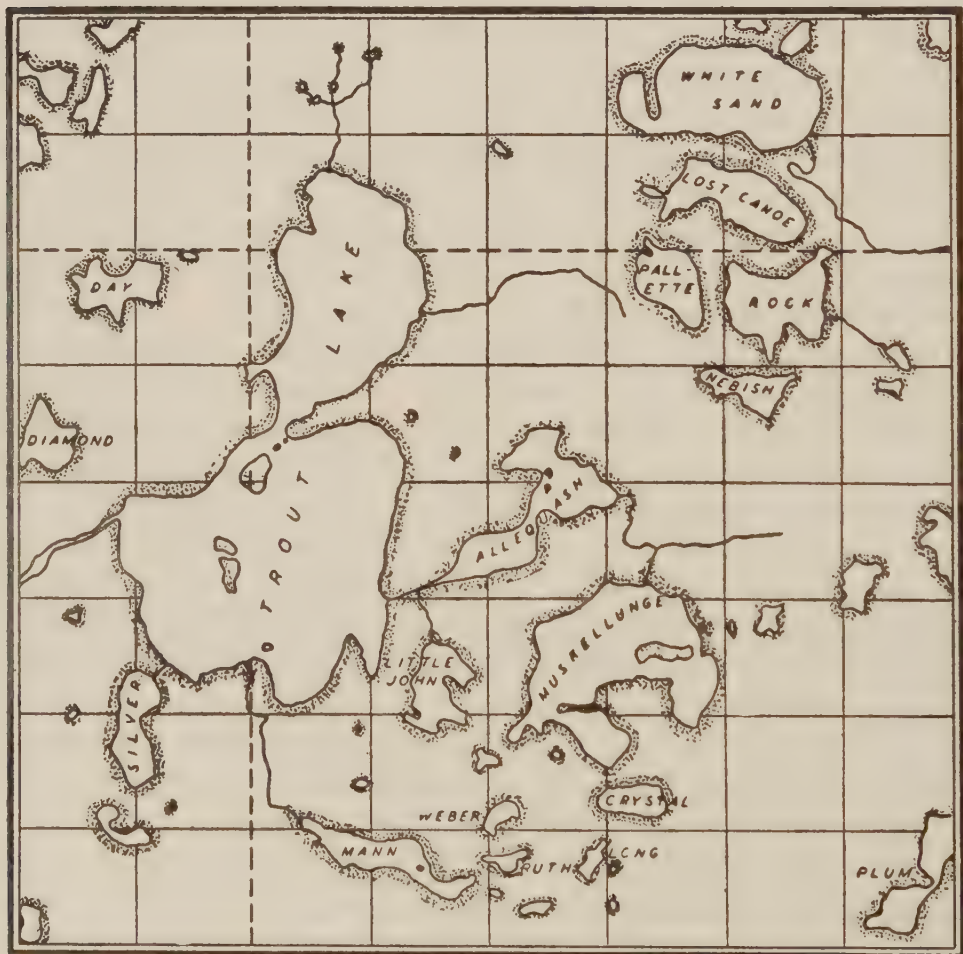


FIGURE 1. Map of Trout Lake region.

Greene (1935) stated that, "Considering its Wisconsin distribution alone, the rock bass could be included among the glacial lake species." Rock bass are particularly abundant in the soft-water lakes of the northeastern highland area.

Nebish Lake is situated in Vilas County, Wisconsin, about 4 kilometers or 2.5 miles east of Trout Lake (the location of the limnological laboratories of the Wisconsin Geological and Natural History Survey) at an elevation of 497 meters or 1,631 feet (Figs. 1 and 2). This small lake, which is completely land-locked, is surrounded by a rather dense second growth of mixed hardwoods and conifers. The water of Nebish Lake is exceptionally soft. Table 1 contains data on the morphometry of Nebish Lake and on the physical and chemical characteristics of its water. Data are given also for Muskellunge Lake and Silver Lake. Certain phases of the life histories of the rock bass populations in these two lakes are considered on pp. 276-288. Other limnological data on Nebish Lake—physical, chemical, and biological—have been presented from time to time in publications of the Survey.

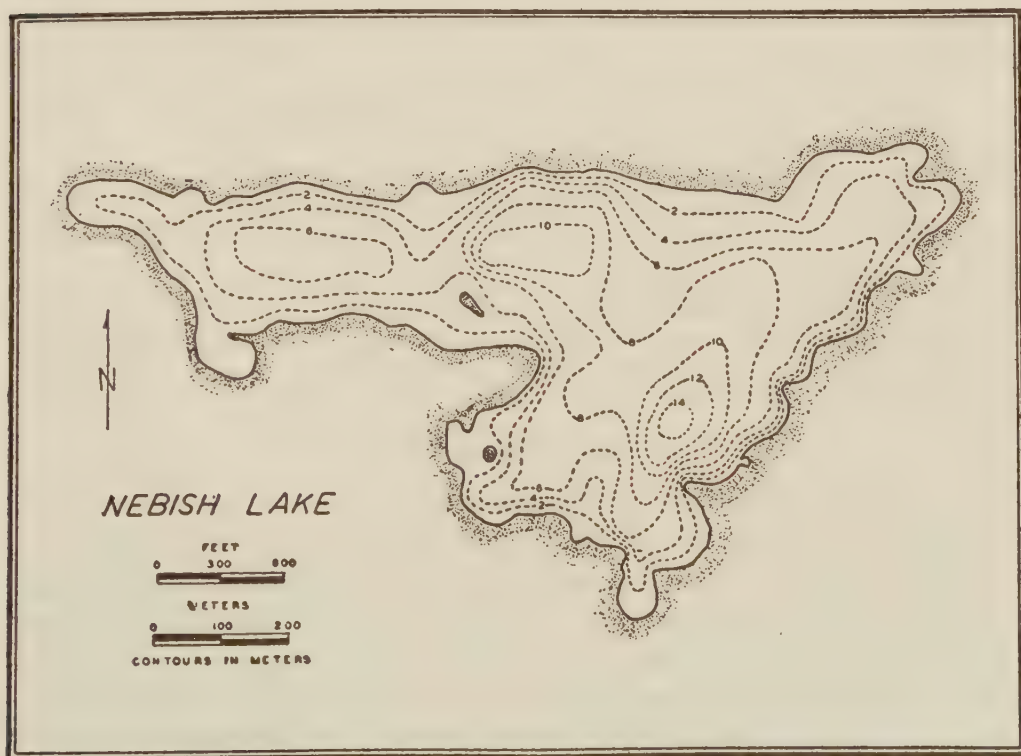


FIGURE 2. Hydrographic map of Nebish Lake.

TABLE 1. *Limnological data for three lakes of the northeastern high-land lake district. The characteristics, transparency, color, pH, conductivity, concentration of bound CO₂, and organic matter of the plankton, refer to average surface conditions in summer.*

Lake	Length, km.	Breadth km.	Area, ha.	Depth in meters		Volume in cubic meters
				Maximum	Mean	
Nebish	1.32	0.66	38.5	15.8	5.2	2,015,000
Muskellunge	3.12	2.00	372.3	21.0	7.0	26,172,000
Silver	1.75	0.66	87.3	19.5	11.3	9,884,000

Lake	Trans- parency, meters	Color	pH	Conduc- tivity, recip. megohms	Bound CO ₂ , mg /l	Plankton, organic matter, mg /l
Nebish	6.0	9	6.8	19	4.0	0.77
Muskellunge	4.0	4	7.2	40	10.0	1.16
Silver	5.5	4	7.5	62	15.0	0.85

Throughout this paper repeated references will be made to certain species of fresh-water fishes by their common names. To avoid misunderstanding that might originate in local variations in the common names of some of these fish the following list of common and scientific names has been prepared:

Bluegill, *Lepomis macrochirus* Rafinesque.
 Cisco, lake herring, *Leucichthys artedi* (Le Sueur).
 Common sucker, *Catostomus commersonnii* (Lacépède).
 Common sunfish, *Lepomis gibbosus* (L.).
 Largemouth black bass, *Aplites salmoides* (Lacépède).
 Long-eared sunfish, *Lepomis megalotis* (Rafinesque).
 Lake Superior long-jaw, *Leucichthys zenithicus* (Jordan and Evermann).
 Muskellunge, *Esox masquinongy* Mitchill.
 Sheepshead, *Aplodinotus grunniens* Rafinesque.
 Smallmouth black bass, *Micropterus dolomieu* Lacépède.
 Whitefish, *Coregonus clupeaformis* (Mitchill).
 Yellow perch, *Perca flavescens* (Mitchill).

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Dr. Hilary J. Deason of the Bureau of Fisheries prepared the diagram of the nomograph presented in Figure 4 and gave helpful advice concerning the preparation of other maps and graphical representations. Dr. Deason also read the original manuscript.

MATERIALS

The study of age and growth of the Nebish Lake rock bass has been based on the determination of age and the calculation of growth histories of 1,215 specimens (Table 2). In addition, the data for 238 fish whose ages were not determined have been employed, when applicable, for the investigation of gill-net selectivity and for the study of the length-weight relationship. The study of the body-scale relationship has included also data for 218 rock bass taken in Muskellunge Lake (p. 207). In addition to the 218 Muskellunge Lake rock bass employed in the study of the body-scale relationship, certain other materials on the fluctuations in the growth and the strength of year classes of rock bass in Muskellunge and Silver Lakes have been presented for comparison with data on the Nebish Lake rock bass.

TABLE 2. *Dates and methods of collection of Nebish Lake rock bass.*

Gear	Date of collection					Total
	July 5 and 6, 1930	August 16 to 21, 1930	July 29 to August 6, 1931	July 12 and August 6 to 11, 1932	August 28, 1935	
Gill nets	..	144	513	492	105	1,254
Hook and line	154	18	2	25	..	199
Total in collection	154	162	515	517	105	1,453
Number aged	..	152	469	493	101	1,215

Certain discrepancies in the number of fish employed in different tabulations should be explained. For example, weights were lacking for 2 of the 154 rock bass collected in July, 1930. Consequently, the table of the length-weight relationship in this collection (Table 56) included only 152 specimens. All 154 were included, however, in the tabulation of the length frequencies of rock bass taken by hook and line (Table 5). Again, the acci-

dental omission of the record of the size of mesh for one fish taken in a gill net reduced the number of fish in Table 3 to 1,004 as compared to the number of 1,005 fish listed in Table 2 as taken in gill nets in 1931 and 1932. The reasons for certain other irregularities in the numbers of specimens will be given later in the paper. It was believed, however, that a preliminary statement as to the occurrence of the discrepancies might save the reader possible annoyance.

METHODS

COLLECTION OF SAMPLES

The collections of the Nebish Lake rock bass were made by hook-and-line fishing and by means of gill nets, as indicated in Table 2. The hook-and-line catches of the different years may be considered roughly comparable, but a complete change of the gill-net equipment was made before the start of the 1931 collecting season.

Nets of only three mesh sizes ($1\frac{1}{2}$, 2, and $2\frac{1}{2}$ inches, stretched measure) were fished² in 1930. The approximate total number of square yards of nets of each size lifted was: $1\frac{1}{2}$ -inch mesh net—954; 2-inch mesh net—1,323; $2\frac{1}{2}$ -inch mesh net—159. All of the gill nets fished in 1930 were in a poor state of repair. The webbing contained many holes and could be torn easily.

The gill nets fished in 1931 and 1932 included the following seven sizes of mesh (stretched measure in inches): $1\frac{1}{4}$, $1\frac{1}{2}$, $1\frac{3}{4}$, 2, $2\frac{1}{4}$, $2\frac{1}{2}$, and 3. Each of these specially constructed nets was approximately 50 yards long by 6 feet deep or had an area of 100 square yards. Lifts were made of 16 gangs of seven nets each in 1931 and of 10 gangs in 1932; thus the fishing efforts for each mesh size in the two years were total lifts of 1,600 and 1,000 square yards, respectively.

The 1935 collection is known to have been taken by means of gill nets, but there are no records³ of the sizes of mesh fished.

All nets were set on the bottom. In 1931 and 1932 the gangs were set, in general, along rather than across the contours, since

² A net of mesh size, $3\frac{1}{4}$ inches, failed to take rock bass.

³ Dr. Clarence L. Schloemer who, along with Dr. William A. Spoor, collected the 1935 materials assures me that several sizes of mesh were included in the gear fished in Nebish Lake in that year.

this procedure gave more reliable information as to the average depth at which the nets were fished. No record was kept in 1930 of the depth at which different nets fished. The nets were lifted every day.

In the collection of fish for biological studies, it is of great importance to know the selective action of the gear employed. Consequently, the Nebish Lake rock bass samples were subjected to detailed analyses which included (1) the tabulation of length frequencies (sexes separately) of the hook-and-line catches and of the catches of gill nets of each size of mesh in each year's collection, and (2) the determination of the average length of the representatives of each age group in the samples taken by nets of each size of mesh and by hook and line. The detailed results of these analyses can not be presented here. However, certain summarizations of the data will give a good idea of the size range of the fish that can be taken by hook and line and by nets of different sizes of mesh.⁴

The gill-net collections of 1931 and 1932 which made up 69 per cent of the total collection (77 per cent of fish used in the study of age and growth) will be considered first. Table 3 shows for the combined collections of the two years the length distribution of the rock bass taken in each mesh size. It is at once apparent that the lower limits of the length ranges of fish that can be taken in different sizes of mesh are rather sharply defined, and that these limits increase regularly with increase in mesh size. The distributions for the smaller mesh sizes, especially those of the 1½-, 1¾-, and 2-inch meshes, are skewed sharply at the lower ends. The absence of this skewness in the distributions of fish taken in the nets with the larger meshes possibly may have depended on the nature of the length distribution of rock bass in the population as a whole (see totals at right of table). Other conclusions to be drawn from the distributions are that nets of each size of mesh fished were able to take fish over a large length range, and that the length-frequency distributions of fish from nets with successively larger mesh sizes have a high percentage of overlap.

⁴ In an earlier paper (Hile, 1936a) data were presented relative to the selective action of gill nets in the collection of samples of ciscoes from lakes of northeastern Wisconsin. This same paper contains a discussion of the general question of gill-net selectivity and gives a review of part of the literature on the subject.

The ineffectiveness of the $1\frac{1}{4}$ -inch mesh for the capture of small fish and the large overlaps among the frequency distributions constitute strong evidence for the adequacy of the sampling over the length range, 75 to 194 millimeters. However, the circumstance that the greatest number of fish was taken in the largest mesh (350 in the 3-inch mesh) suggests the possibility that the use of a net of still larger mesh size would have been advisable.⁵ There is reason to believe, nevertheless, that the use of nets with larger meshes would have increased the number of

TABLE 3. *Length frequencies of Nebish Lake rock bass taken in different sizes of gill-net mesh, sexes and all age groups (including fish not aged) combined for 1931 and 1932.*

Length interval in millimeters	Gill-net mesh (stretched measure)							Total
	$1\frac{1}{4}$ inches	$1\frac{1}{2}$ inches	$1\frac{3}{4}$ inches	2 inches	$2\frac{1}{4}$ inches	$2\frac{1}{2}$ inches	3 inches	
200—204	..	..	..	..	1	1	1	3
195—199	..	..	..	..	..	..	3	3
190—194	..	1	2	..	..	2	13	18
185—189	..	..	..	3	..	5	40	48
180—184	..	1	1	1	4	14	70	91
175—179	..	..	2	..	6	13	100	121
170—174	..	..	1	5	8	34	84	132
165—169	..	..	..	3	5	24	30	62
160—164	..	..	1	9	10	45	5	70
155—159	..	1	1	2	6	36	2	48
150—154	..	..	1	2	6	32	..	41
145—149	..	..	..	1	4	12	1	18
140—144	..	2	..	4	5	5	..	16
135—139	..	..	..	3	6	1	..	10
130—134	..	..	1	2	6	..	..	9
125—129	1	1	1	6	2	..	..	11
120—124	1	..	7	22	1	..	..	31
115—119	..	1	7	21	..	..	1	30
110—114	1	2	15	6	..	..	..	24
105—109	..	2	12	1	..	..	..	15
100—104	..	7	17	1	..	..	..	25
95—99	..	10	8	..	..	..	..	18
90—94	..	53	2	..	..	..	..	55
85—89	1	69	..	..	..	..	..	70
80—84	6	22	..	..	..	..	..	28
75—79	5	..	..	..	..	..	..	5
70—74	2	..	..	..	..	..	..	2
Total number	17	172	79	92	70	224	350	1,004
Average length	86	92	116	134	156	162	177	147

⁵ A $3\frac{1}{4}$ -inch mesh net fished in 1930 failed to take rock bass; however, the older age groups were represented more strongly in 1931 and 1932 than in 1930.

large fish taken but would not have brought about any important upward extension of the general length distribution. The frequency distribution of fish captured by the 3-inch mesh net is much more compact than are the distributions for nets of smaller mesh. Seemingly the 3-inch mesh net did not share the capacity of nets of other mesh sizes to take fish of lengths well above the lower limit of effectiveness. The compact distribution of the lengths of rock bass from the 3-inch mesh gill net can be explained, however, on the logical assumption that the absence of larger fish in the catch was caused by their absence from the lake. This assumption is supported by the observation that fish longer than 190 millimeters usually are very old (p. 223). It seems valid to conclude, therefore, that the use of nets with meshes larger than 3 inches might have changed somewhat the numerical representation of the older age groups but would not have affected the determination of their growth histories.

Among the smaller fish the growth data for age-group II (this age group was the youngest in the collections—see Tables 12 and 13 for the frequency distributions of the group) were discarded as unreliable, but the rejection was based on direct observations of the fishing action of gill nets rather than on the analysis of gill-net catches. It was observed repeatedly that small fish appeared to penetrate the meshes of gill nets with difficulty, and that ordinarily the smaller the fish the less securely it was held. Possibly these small fish do not swim with sufficient vigor to force their way into the meshes. At any rate, the suspicions concerning the reliability of the II-group samples were verified by the comparison of the growth of II-group rock bass with the growth of older age groups of the same year classes. The II group was the only age group excluded from the computation of general growth curves.

The collection of August, 1930, (Table 4) which was taken with nets of only three sizes of mesh is admittedly less satisfactory than the gill-net samples of 1931 and 1932. Particularly unfortunate was the low fishing intensity of the 2½-inch mesh net (p. 194). The addition of the 18 rock bass taken by hook and line in August, 1930, (Table 5) doubtless strengthened the representation of the larger fish. Since the growth data obtained from the collection of August, 1930, did not disagree seri-

ously with those of other years (Tables 14 and 15) this collection was retained as part of the general growth material.

The hook-and-line catches formed an unimportant part of the general growth material. Their length distributions (Table 5) resemble those of the rock bass from the gill nets with the larger meshes ($2\frac{1}{4}$ and $2\frac{1}{2}$ inches).

TABLE 4. *Length frequencies of Nebish Lake rock bass taken in different sizes of gill-net mesh in August, 1930, with the sexes and all age groups combined (including fish not aged).*

Length interval in millimeters	Gill-net mesh (stretched measure)			Total
	$1\frac{1}{2}$ inches	2 inches	$2\frac{1}{2}$ inches	
170—174	2	5	1	8
165—169	..	4	1	5
160—164	1	5	1	7
155—159	..	3	6	9
150—154	..	14	5	19
145—149	2	12	3	17
140—144	2	7	3	12
135—139	..	5	..	5
130—134	..	7	..	7
125—129	..	2	..	2
120—124	..	10	.	10
115—119	..	12	.	12
110—114	2	..	..	2
105—109	2	..	..	2
100—104	1	..	..	1
95—99	2	..	..	2
90—94	1	..	..	1
85—89	4	..	..	4
80—84	10	..	..	10
75—79	8	..	..	8
70—74	1	..	..	1
Total number	38	86	20	144
Average length	99	142	154	132

As stated previously (p. 194), there are no records concerning the meshes of the gill nets fished in 1935. The age composition of the collection was unusual (p. 245), but the good agreement of the data on the growth of the different age groups with data for corresponding age groups of earlier collections (Tables 14 and 15) appears to justify the retention of the 1935 sample as part of the general growth material.

TABLE 5. *Length frequencies of rock bass taken by hook and line, 1930 to 1932, with the sexes and all age groups combined (including fish not aged).*

Length in- terval in millimeters	Date of collection				Total
	1930		1931	1932	
	July ¹	August			
180—184	2	1	..	..	3
175—179	14	..	..	3	17
170—174	30	1	2	3	36
165—169	24	1	..	7	32
160—164	36	3	..	5	44
155—159	28	3	..	2	33
150—154	13	4	..	2	19
145—149	2	2	..	..	4
140—144	3	3	..	1	7
135—139	2	..	..	..	2
130—134	..	..	..	..	..
125—129	..	..	..	1	1
120—124	..	..	..	..	..
115—119	..	..	..	1	1
Total number	154	18	2	25	199
Average length	164	156	172	161	163

¹ This collection not employed in the study of age and growth.

RECORDS FOR INDIVIDUAL SPECIMENS

Scale samples were taken at the field laboratory from all rock bass except those preserved for a study of the body-scale relationship. (For treatment of preserved specimens see p. 207.) The scales were removed from the left side of the body in the region between the lateral line and the spinous portion of the dorsal fin, and were stored in Bureau of Fisheries scale envelopes. On each serially numbered envelope were recorded the date, name of the lake, length, weight, sex, state of maturity, and gear.

The standard length (from the tip of the snout to the base of the caudal peduncle) was measured for every fish. Measurements of total length (from the tip of the snout to the line connecting the tips of the extended caudal fin⁶) were made for the 1930 collections only. All length measurements were made with

⁶ Subsequent experiences have convinced me that the most reliable and practical measurement of total length is the maximum measurable length, that is, the length from the extreme anterior point of the head to the extreme end of the caudal fin with its upper and lower edges parallel. This maximum length is the only one admissible when questions of legal minimum total length are concerned.

a steel tape in a straight line between the points indicated and were recorded to the nearest millimeter.

The fish were weighed on a Chatillon spring platform balance with a 500-gram capacity and calibrated by 2-gram intervals. Weights were estimated to the nearest gram. During the latter part of the 1931 season the balance developed a fluctuating error that at no point exceeded 2 grams. No corrections were attempted for the error, but the defective balance was replaced by a new instrument at the start of the 1932 season. This new balance was still in use in 1935.

In 1930 and 1931 the smaller individuals with poorly developed gonads were designated as immature without record of sex. A more careful examination provided sex records for every individual of the 1932 and 1935 collections.

PREPARATION AND EXAMINATION OF SCALE SAMPLES

The scales were soaked in water and cleaned by means of a dissecting needle and a small brush. Three scales from each fish were mounted on a microscope slide in a glycerin-gelatin medium.⁷ Care was taken to avoid scales with regenerated centers or of highly asymmetrical or otherwise irregular form. On the label of each slide were recorded field number, slide number, length, weight, sex, maturity, and gear. The scales of all of the 1930 and 1931 samples and of about one-third of the 1932 collection were examined at a magnification of $\times 40.5$ by means of the projection apparatus described by Van Oosten (1923). The remaining scales of the 1932 collection were studied at a magnification of $\times 40.7$ with the aid of the apparatus described by Van Oosten, Deason, and Jobes (1934).

DETERMINATION OF AGE

The determination of the age of the rock bass from scale examinations has been based on the counting of the number of annuli or lines of discontinuity between the growth areas of successive years. Fish whose scales are without annuli, that is, fish in the first year of life, are designated as members of the O group. The ages of the older fish are expressed by Roman

⁷ The formula for the medium was given by Van Oosten (1929).

numerals corresponding to the number of annuli or completed years of life. Thus a fish in its second year of life (with one annulus) is a member of age-group I, a fish in its third year of life (with two annuli) belongs to the age-group II. . . . Fish hatched in the same calendar year are members of the same year class regardless of their age at capture. For example, the 1930 VII group, the 1931 VIII group, and the 1932 IX group are all 1923 year-class fish.

Since the rock bass scale is typically ctenoid, the annulus ordinarily can be traced only through the anterior portion of the scale. A few scales were seen that had not yet formed ctenii as late as the sixth or seventh year of life, but many form ctenii in the first summer. Differential wear of the ctenii, dependent on the age of that portion of the scale on which they occur, sometimes gives a clue to the position of the year-mark in the posterior field. In general, however, the differential wear of the ctenii is of no assistance in the determination of age.

VALIDITY OF THE ANNULUS AS A YEAR-MARK

The validity of the annulus as a true year-mark has been proven for so many species of fish, both marine and fresh-water, that the examination of scales as a general method for the determination of age in fishes may be considered well established. Any historical or critical review of the subject in this paper would be without point. Theoretical considerations of the validity of age determinations from scale study will be limited, therefore, to a demonstration of the applicability of the method to the rock bass.

The following outline of the most important arguments in favor of the validity of the annulus in rock bass scales as a true year-mark is based on data that will be presented in later sections of this paper. Similar arguments have been given for so many species that discussion will be held to a minimum.

(1) *Correlation between age and size.*—(a) The regularity with which increase in the number of annuli is accompanied by increase in the size of the fish proves that the occurrence of annuli on the scales is not haphazard but that annuli are added systematically as growth proceeds. Furthermore, fish assigned to the same age group have similar lengths (Table 9 and 10).

(b) Modes in the length-frequency distributions of small fish coincide with the modal lengths of age groups based on scale reading. In the Muskellunge Lake collections of small fish (see p. 207 and Table 6) all individuals in the length interval, 15 to 39 millimeters, were without annuli, and all fish in the length interval, 50 to 59 millimeters, had one annulus. The smaller of these two groups could hardly be interpreted as other than the young of the year. (One 15-millimeter fish was without scales on a large portion of its body.) The next larger group would then logically be expected to be second-year fish, with one annulus. In the Nebish Lake collections (Tables 12 and 13) age-group II forms a distinct mode in the general length-frequency distribution of each sex.

(2) *Agreements among calculated growth histories.*—(a) Lengths at the end of the various years of life calculated from scale measurements⁸ (Tables 14 and 15) agree well with the corresponding empirical lengths⁹ of younger age groups whose ages were determined by the examination of scales. In general, this agreement serves merely to establish the annulus more certainly as a structure whose appearance on the scales follows a definite systematic pattern (*cf.* argument 1a). However, the agreement of lengths calculated from scale measurements of older fish with the empirical lengths of younger fish whose ages were determined by modes in the length-frequency distributions (see argument 1b) does provide an argument for the yearly formation of annuli.

(b) There is a generally good agreement among the data on the calculated growth of fish of the same age groups in different years' collections and among the data for different age groups of the same or different years' collections, but *a still better agreement is to be found among the growth histories of the different age groups of the same year class*. As a specific illustration, the agreement among the growth histories (Tables 14 and 15) for both the males and females of the 1930 VII group, the 1931 VIII

⁸ The method of calculation is described on pp. 206-217.

⁹ Empirical lengths of age groups usually fall between two calculated lengths. For example, average actual lengths for IV-group fish usually will fall between the calculated lengths at the end of the fourth and fifth years of life. This situation is to be expected since all collections were made during the growing season.

group, and the 1932 IX group, all purportedly members of the 1923 year class, is closer than the agreement among the VII groups, the VIII groups, or the IX groups of the same sex collected in different years. In fact, the corresponding calculated lengths of the heavily represented age-groups VIII and IX of the 1923 year class are well-nigh identical. That the growth data for different age groups of the same year class should agree so closely is understandable, indeed is to be expected, since all age groups were hatched in the same year and were, therefore, subjected to the same environmental conditions at the same periods of their life histories. The point to be stressed is that the identification of these so clearly homogeneous groups was based on scale readings. The 1932 IX group of each sex had a growth curve almost identical with that of the same sex of the 1931 VIII group but the IX-group fish had one more annulus. The obvious deduction is that an annulus was laid down during the 1-year interim between the 1931 and 1932 collection dates. Further examination of Tables 14 and 15 will reveal a tendency for growth histories of other well represented age groups to conform to a more or less typical "year-class curve".

(c) The agreement among different year classes as to the goodness or poorness of growth in certain calendar years provides another argument for the interpretation of the annulus as a year-mark (see pp. 249-259). The growth in 1928 will serve as an example. In that year the growth of male rock bass (Table 24) in every year of life from the second to the eighth, inclusive,¹⁰ was below average for fish of corresponding age. Thus the data for every year class from 1921 to 1927, inclusive, indicate 1928 to have been a poor-growth year. The results are similar for the female rock bass (Table 25). Here again the 1928 growth was below average for all years of life from the second to the eighth (represented by year classes 1921 to 1927). The relatively good ninth-year growth of the females of the sparsely represented 1920 year class provides an unimportant exception to the trend of the data.

The designation of 1928 as a poor-growth year was based on scale readings that assumed the annulus to be a true year-mark.

¹⁰ First-year growth must be considered separately from growth in later years (p. 259).

Consequently, the uniformity of the results obtained independently from seven year classes, each of which was represented by two or more age groups, must be construed as a powerful argument for the contention that annuli are formed at the rate of one per year. The argument is strengthened materially by the close agreement between the data for the sexes.

The continued examination of Tables 24 and 25 will reveal similar general agreement among year classes as to goodness or pooriness of growth in other calendar years. Furthermore, the data for the sexes agree well for the individual years.

(3) *Persistent abundance or scarcity of certain year classes.*—The persistent abundance or scarcity of a year class in the collections of successive calendar years provides possibly the most convincing evidence for the interpretation of the annulus as a year-mark. In the rock bass data the exceptionally rich 1923 year class offers the outstanding example of continued high abundance (Table 23). This year class as age-group VII was dominant (38.2 per cent) in the 1930 samples. Now, if the scale readings are accurate measures of age, this same year class should be strong in the 1931 collections also, but the number of annuli should be eight. The 1931 data conform precisely with this expectation, for in that year the 1923 year class as age-group VIII made up 45.8 per cent of the total collection. The unusual numerical strength of rock bass of the 1923 year class extended into 1932, in which year as age-group IX they were exceeded in abundance only by age-group II and were by far the strongest of the older age groups.

The great abundance of the 1923 year class in the collections of three successive calendar years is important not only for its contribution to the proof that the annulus on the rock bass scale is a true year-mark, but also as a demonstration that the determination of age in the Nebish Lake rock bass is practicable up to a relatively high age.

Other year classes, in contrast to the 1923 year class, were consistently weak at all ages at which they were collected. The 1927 year class provides an outstanding example.

The evidence outlined in the preceding pages leaves little room for doubt concerning the validity of the annulus on the

scales of rock bass as a true year-mark. However, the demonstration of the general reliability of age determinations in the rock bass does not mean that fully dependable readings can be made from the scales of every individual. The difficulties that were encountered in the interpretation of some scales will be discussed in the following section.

DIFFICULTIES ENCOUNTERED IN THE DETERMINATION OF AGE

False annuli or accessory checks, which cause so much difficulty in the interpretation of the scale structure of some fish, are of rare occurrence in the scales of the Nebish Lake rock bass. This situation is most fortunate in view of the abundance of old fish in the collections. Nevertheless, a few fish were discarded because of the inability to decide whether certain checks were actually annuli.

The erosion or resorption of portions of the scales of certain older individuals accounted for a large part of the difficulties experienced in the determination of age. The appearance of these defective scales suggested that the periphery had been resorbed at some earlier age. In some of the eroded scales only the lateral regions were affected, but in others erosion evidently had occurred along the entire periphery of the imbedded portion of the scale. The former, less severe, type of erosion made it impossible to trace certain annuli throughout their entire courses, but frequently did not prohibit a reasonably reliable assessment of age. On the other hand, all scales with the more complete erosion had to be discarded. Not only were the age readings of these scales questionable, but the earlier loss of portions of the scales along the anterior edge made their measurements worthless for the calculation of growth.

The examination of the scales failed to connect the occurrence of erosion with any particular calendar year, although most of the erosion appears to have occurred prior to 1931. It was observed also that scale erosion ordinarily does not occur before the sixth year of life. None of the fish had scales whose edges were eroded at the time of capture.

Late formation of the annulus may be a source of difficulty in the scales of fish that are caught early in the growing season. The collection of July 5 and 6, 1930, contained some fish whose scales obviously had newly-formed annuli or annuli in the proc-

ess of formation, and others whose scales had developed bands of growth of varying width outside the last visible annulus. Since it was uncertain for many of the latter group whether the band of growth represented growth made in 1930 subsequent to annulus formation, or whether the 1930 annulus had not yet been formed, the collection was rejected for purposes of age determination. The only other collection taken in the first half of July was one of 25 fish captured by hook and line on July 12, 1932. All of the individuals of this collection had recently-formed annuli lying just inside the margins of the scales. There is no reason to believe that late annulus formation had any effect on the accuracy of the age determinations for fish taken in late July or in August.

In all the collections combined (exclusive of the July, 1930, sample), 95.5 per cent of the scales were read. The percentages for the different years were: 1930 (August collection)—95.6 per cent; 1931—93.6 per cent; 1932—96.7 per cent; 1935—99.0 per cent. These percentages are higher than would be obtained from the data for "Number aged" and "Total in collection" listed in Table 2. The discrepancy has its origin in the exclusion from consideration of those fish represented by regenerated scales in the sample.

BODY-SCALE RELATIONSHIP AND THE CALCULATION OF GROWTH

Scale measurements for the purpose of computing individual growth histories were made for every rock bass whose age was determined. The distance from the center of the focus to each annulus and to the extreme anterior edge of the scale was measured on the projected image of one scale¹¹ from each rock bass. The measurements were made by means of an accurately graduated ruler, whose edge was laid along the radius most nearly collinear with the focus, and were recorded to the nearest millimeter (occasionally to the half-millimeter).

Computations of individual growth histories from scale measurements have been made for many species and by a variety of methods. Although a review of the general problem of the computation of growth from scale measurements would not be

¹¹ Three scales were measured for most of the fish employed in the study of the body-scale relationship (p. 209).

desirable in this paper¹², it may be stated that the cumulative experience of numerous investigators points more and more to the conclusion that there is no general solution of the problem. The relationship between body growth and scale growth appears to vary widely from one species to another. Consequently each species of fish (and possibly different varieties or populations within a species) presents its own special problem as to the method to be followed for the calculation of growth. Accordingly a detailed study of the body-scale relationship in the rock bass was undertaken in order to determine the most satisfactory method for the computation of growth histories in this species.

The determination of the relationship between the body length of the rock bass and the length of the anterior radius of the scale was based on the measurements of selected or "key" scales from 318 fish. Of this total, 100 specimens were taken in Nebish Lake and 218 were captured in Muskellunge Lake (Fig. 1 and Table 1). All the specimens less than 86 millimeters long came from Muskellunge Lake. The Nebish Lake rock bass were taken by gill nets on August 6 and 8, 1932. The Muskellunge Lake fish of a length of 79 millimeters or more were taken in gill nets on July 24, 25, and 28, 1932. The smaller Muskellunge Lake rock bass were taken by means of a small hand seine on various dates during the latter half of August, 1932.

The fish from both lakes that were taken in gill nets were weighed and measured when fresh, provided with individual, serially numbered tin tags, and preserved in a 10 per cent solution of formalin. Upon their arrival at the Ann Arbor laboratory the specimens were soaked about 4 days in water and then transferred permanently to a 70 per cent solution of alcohol. The smaller Muskellunge Lake rock bass were not measured when fresh and were preserved directly in alcohol. The length measurements of these smaller preserved fish were corrected for shrinkage produced by the preservative.¹³

¹² Excellent historical and critical reviews of the subject may be found in publications by Van Oosten (1929), Graham (1929), and others.

¹³ It was assumed that the correction factor, 1.015, which was determined from the remeasurement of the larger (79 millimeters and longer) Muskellunge Lake specimens was applicable to the smaller preserved fish. At the time of the remeasurement of the large preserved fish (October 10 and 11, 1932) they had been in alcohol about 5 weeks. The measurements of both the fresh and preserved fish were made by the same individual (Dr. Edward Schneberger).

TABLE 6. *Average length of the anterior radius ($\times 40.5$) of key scales of rock bass at different body lengths as determined from the combined collections from Nebish and Muskellunge Lakes, 1932.*

Number of fish	Standard length in millimeters	Anterior scale radius in millimeters ($\times 40.5$)	Number of fish	Standard length in millimeters	Anterior scale radius in millimeters ($\times 40.5$)	Number of fish	Standard length in millimeters	Anterior scale radius in millimeters ($\times 40.5$)
5	18.3	4.5	15	96.9	53.9	6	151.0	103.0
10	23.2	8.9	22	101.6	59.9	9	156.3	113.3
41	28.0	9.8	8	106.1	63.6	8	162.4	125.1
32	32.0	11.8	13	110.9	70.1	10	167.9	125.3
9	53.2	24.7	4	117.5	79.9	10	171.7	114.2
1	58.9	31.5	12	121.6	80.7	5	176.6	127.8
1	72.1	38.5	7	126.9	83.4	8	182.2	135.8
1	79.0	42.5	6	130.9	95.2	5	186.4	146.2
12	82.3	46.0	2	139.0	102.4	2	190.5	133.1
20	87.1	47.5	10	141.8	94.4	2	197.5	143.5
16	91.1	50.3	4	146.5	101.0	2	203.5	160.8

The key scales taken from each specimen were removed from the second scale row above the lateral-line row, and were the three scales immediately posterior to the scale lying directly above the twelfth lateral-line scale. It was from this general region that the unselected scales of the general collections were taken. Ordinarily the key scales were taken from the left side, but in those specimens whose scales on this side had regenerated centers, the key scales were removed from the right side. Even so, a few fish had only one or two measurable key scales or none at all. The method of mounting and measuring the key scales was the same as that described previously (p. 206) for the scales in the general collection. The scale length for each fish was determined as the mean of the measurements of its key scales.

In the O-group fish, whose length ranged from about 15 to 35 millimeters, the individual scales were so small that it was not possible to remove and mount the key scales individually. In these fish a small patch of scales from the key area was detached with a dissecting needle and mounted. The number of measurable scales (scales not folded or torn) obtained by this method varied from two to five and all were measured and the measurements were averaged for each individual.

Table 6 shows the relationship between body length (averages for 5-millimeter intervals) and the length of the magnified anterior scale radius of the Nebish Lake and Muskellunge Lake rock bass, with the sexes and all ages combined. This general combination of data was made only after a detailed examination of the variation of scale length with body length by age and by sex for the lakes separately failed to reveal consistent differences among the several categories.

The plotting of the original data on both absolute and logarithmic scales suggested at once that the mathematical relationship between body length and scale radius in the rock bass might be described by the equation for the parabola:

$$L = cS^n, \quad (1)$$

where

L = body length,

S = anterior scale radius,

and

c and n = constants.

Accordingly, an equation of this type was fitted to the em-

pirical data on body length and scale radius. The resulting equation was:

$$L = 5.84011 S^{0.695992}, \quad (2)$$

or in the logarithmic form,

$$\log L = 0.7664210 + 0.695992 \log S. \quad (3)$$

A comparison of the curve for equation (2) with the averages¹⁴ of the empirical data may be had from the examination of Figure 3. It may be seen that the theoretical curve fits the empirical data rather closely. The most serious disagreement is

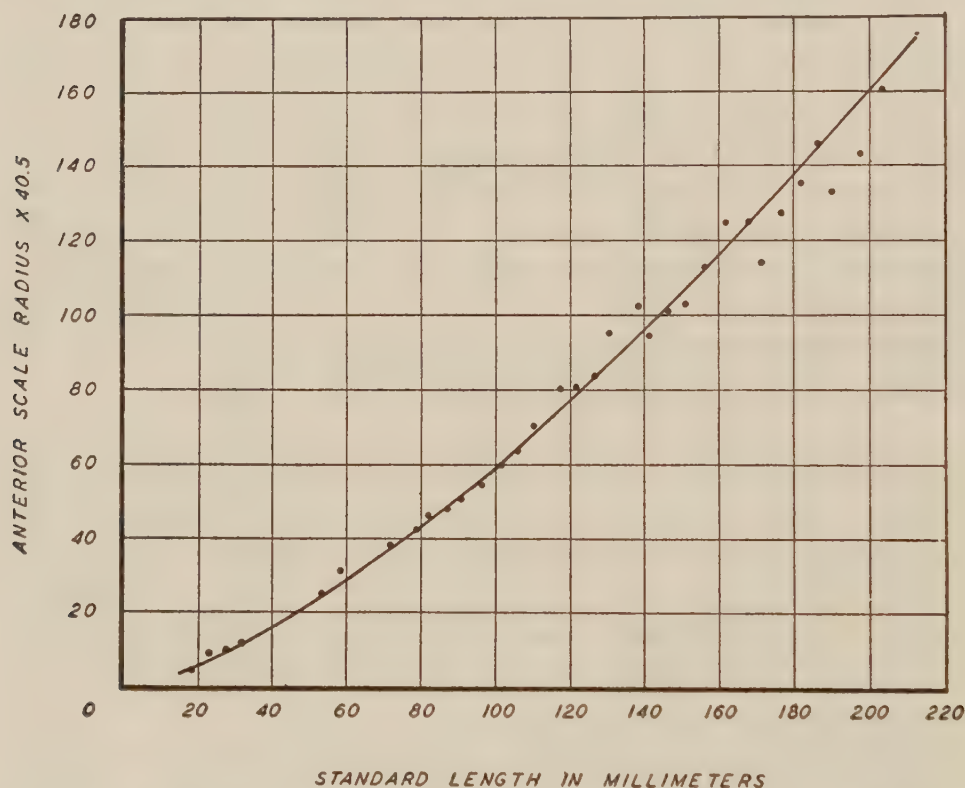


FIGURE 3. Relationship between the length of Nebish Lake rock bass and the length of the anterior radius of (magnified) key scales. The curve is the graph of the equation fitted to the data on body length and scale length (radius). The dots represent the empirical averages of body length and scale length (radius).

¹⁴ Equations (2) and (3) were not derived from the averages presented in Table 6. In the derivation of the equations the measurements for each individual fish were considered as a point, and a straight line was fitted to the logarithms of the individual body lengths and anterior scale radii. It does not appear desirable, however, to present the data for the individual specimens.

to be found in the region where the fish length exceeds 170 millimeters. At these higher lengths the empirical points tend to lie to the right of the curve, but most of these points are represented by very small numbers of fish.

Since the parabolic equation (1) describes satisfactorily the body-scale relationship of the rock bass from Nebish and Muskellunge Lakes, it may be stated for these populations that from the time of scale formation¹⁵ (at a body length of about 15 millimeters): (1) The growth of the scale with increase in the length of the fish proceeds along a curve whose backward continuation passes through the origin; and (2) the relative rates of growth of body and scale maintain a constant ratio.

For the computations of individual growth histories of rock bass a table of solutions of equation (2) was prepared. This table contains the body lengths (computed to the nearest tenth of a millimeter) corresponding to half-millimeter intervals of scale length.¹⁶ Although the computed lengths in individual growth histories were recorded only to the nearest millimeter, the tabular solutions to the nearest tenth of a millimeter facilitated the reading of lengths corresponding to the "corrected" scale measurements, to be described presently. It has not been considered desirable to present this detailed table of solutions.

The procedure followed in the computation of growth histories will be illustrated by two examples (Table 7). The fish selected were both VIII-group males from the 1931 collection, and both were 183 millimeters long (standard length) at capture. For convenience they may be designated by their slide numbers, 263 and 322.

The magnified radius of the scale measured from the slide for fish No. 263 was 128 millimeters. The radial measurements to the first, second, third, . . . annuli were 17, 33.5, 52, . . . millimeters respectively. However, the scale that was measured was

¹⁵ The "time of scale formation" as used here refers to the time at which the scale has attained sufficient size that it can be removed from the fish, mounted, and measured.

¹⁶ Actually equation (1) was solved for 5-millimeter intervals of the magnified scale radius and the solutions for the intervening points were obtained by interpolation. For a large part of the curve only linear interpolation was needed in order to arrive at solutions that were accurate to the nearest tenth of a millimeter. At the lower lengths, however, the use of second differences—and for a few intervals, third differences—proved necessary.

TABLE 7. *Original scale measurements, corrected scale measurements, and calculated lengths at the end of each year of life for two rock bass of the 1931 VIII group.*

Year of life	Specimen No. 263			Specimen No. 322		
	Scale measurement	Corrected scale measurement	Calculated length	Scale measurement	Corrected scale measurement	Calculated length
1	17	18.7	45	15	12.7	34
2	33.5	36.9	72	41	34.6	69
3	52	57.3	98	75	63.4	105
4	64	70.5	113	100	84.5	128
5	86	94.8	139	116	98.0	142
6	106	116.8	160	138	116.6	160
7	116	127.8	171	152	128.4	171
8	125	137.8	180	161	136.0	178
8+	128	141.1	¹ 183	167	141.1	¹ 183

¹ Length at capture.

smaller than would be expected, on theoretical grounds, on a fish 183 millimeters long. Consequently, these several measurements require correction before they can be employed for the determination of the lengths of fish No. 263 at the end of the different years of life. The table of solutions for equation (2) contains the following solutions for fish whose lengths are approximately 183 millimeters long:

Scale radius	Fish length
141.0	182.9
141.5	183.4

It is obvious therefore that the theoretical length of the scale from fish No. 263 is 141.1 millimeters as compared with the measured length of 128 millimeters. The ratio between the two scale lengths, $141.1/128 = 1.102$, may be used as a factor to "correct" or adjust the original scale measurements to the theoretical level. For example, $1.102 \times 17 = 18.7$; $1.102 \times 33.5 = 36.9$; $1.102 \times 52 = 57.3$; . . . and finally to verify the accuracy of the correction, $1.102 \times 128 = 141.1$. The use of the "correcting factor" involves the assumption that the percentage or relative deviation of the length of the anterior radius of any single scale from the theoretical length of the radius is constant at the time of formation of all annuli. There appears to be no alternative to this assumption although admittedly it is unproven.

The calculated lengths of fish No. 263 at the end of different years of life are simply the solutions of equation (2) corresponding to the corrected scale measurements. For example, the solution at $S = 18.7$ (end of first year) falls between the tabular solutions, $L = 44.5$ when $S = 18.5$, and $L = 45.4$ when $S = 19.0$. The length of fish No. 263 at the end of the first year of life may therefore be seen at a glance to have been 45 millimeters. Similarly the solution for $S = 36.9$ falls between the points (36.5, 71.4) and (37.0, 72.1), and $L_2 = 72$ millimeters. The remaining solutions are read from the table in the same manner.

Precisely the same procedure was followed in the calculation of the growth history of fish No. 322. Here, however, the scale that was measured proved to be larger than the theoretical scale (167-millimeter anterior radius as compared with the theoretical radius of 141.1 millimeters). The original measurements were reduced therefore by the factor, $141.1/167 = 0.845$. Again the solutions corresponding to the corrected scale measurements are obtained from the table of solutions of equation (2).

In actual practice the corrected scale measurements need not be recorded. Instead, the correcting factor, theoretical scale length/measured scale length, is placed in the keyboard of a calculating machine and multiplied successively by the several scale measurements. The solutions (calculated lengths) corresponding to the corrected scale measurements are read from the table of solutions and recorded at the time each corrected measurement is obtained.

The correction of the original scale measurements can be made satisfactorily also by means of a simple nomograph (Fig. 4) which consists of a thin spring-steel ruler graduated by tenths of an inch lying on a background of 0.1-inch¹⁷ cross-section paper. (The use of the nomograph involves only the horizontal rulings of the paper.) The slotted end of the ruler is mounted on a flat brass cylinder set flush in the board on which the paper is mounted and is held in position by a small bolt fitted with a washer and a wing nut. For the computation of the corrected scale lengths for fish No. 263 the ruler is placed in such a position that the 0 graduation of the paper coincides with the 0 grad-

¹⁷ The use of rather large graduations guarantees greater accuracy and reduces fatigue.

uation of the ruler, and the 128 (= 12.8 inches) horizontal line falls slightly beyond the 141 (= 14.1 inches) graduation of the ruler. The wing nut is then tightened and the corrected scale measurements are read from the ruler at the points of intersection with the horizontal rulings corresponding to the original scale measurements. The procedure for fish No. 322 is similar. The 0 graduations are again made to coincide, and the 167 grad-

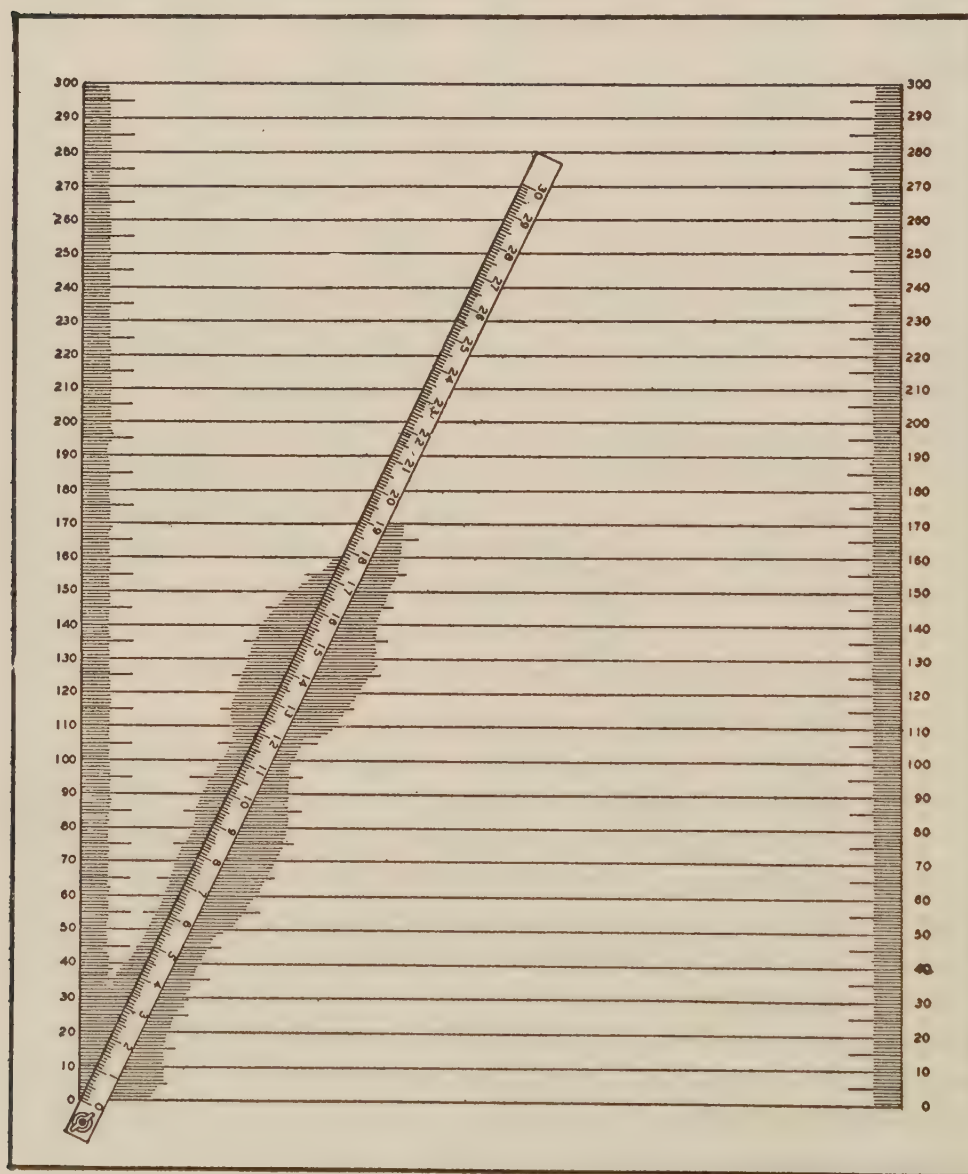


FIGURE 4. Diagram of nomograph employed for the correction of scale measurements. See text for explanation.

uation of the ruler is made to fall slightly beyond the 141 horizontal line. This time, however, the corrected measurements are read from the paper at the points of intersection with the original scale measurements along the ruler. The correcting factors discussed on p. 212 are merely the sines or cosecants of the angles at which the ruler in its different positions crosses the horizontal rulings.

Comparisons with machine calculations revealed that the nomograph gave accurate results. The only disagreements between the calculated lengths based on scale corrections from the nomograph and on scale corrections by machine occurred when the calculated lengths ended almost exactly in a half-millimeter.

The method employed for the calculation of individual growth histories of the rock bass may be considered in a sense a combination of methods used previously by Monastyrsky (1930) and Segerstråle (1933). The mathematical relationship assumed to exist between body length and scale radius in the rock bass (namely, that of a logarithmic straight line) is the one which Monastyrsky applied to several species and which he held to be generally applicable. However, Monastyrsky did not use a tabulation of corresponding body and scale lengths, but performed his growth calculations by means of a nomograph with logarithmic scales. Segerstråle made growth calculations with the aid of tables of body lengths and scale lengths (based on measurements of "normal" or key scales) and "normalized" his original scale measurements in a procedure identical with the "correction" of the measurements of rock bass scales. Segerstråle's tabulations of the body-scale relationship differed from that made for the rock bass in that his data were purely empirical and did not involve an assumption of any definite mathematical relationship between body length and scale length.

The only previously published growth calculations of rock bass (Wright, 1929) were made by the direct-proportion method, that is, on the assumption that the ratio, body length/scale radius, is constant for all lengths of fish beyond that at which the first annulus is laid down. Wright recognized the probable inaccuracy of his method of growth calculation and stated that it "... is believed to give only approximate results ..."

The comparison of the growth histories of nine age groups of Nebish Lake rock bass (age-groups II to X of the males of the 1931 collection) as calculated by direct proportion and from equation (2) provides a measure of the error involved in the former method (Table 8). It may be seen that the extent of the error depends both on the length at capture of the fish for which the calculations are made and on the year of life for which the calculations are made. Although there are a few minor exceptions it may be said that in general the differences between "corrected" and "uncorrected" calculated lengths for corresponding years of life tended to decrease with a decrease in the size (at capture) of the fish on which the calculations were based. Within the individual age groups these differences tended first to in-

TABLE 8. Comparison of the growth histories of nine age groups of male Nebish Lake rock bass captured in 1931 as computed from scale measurements by direct proportions (uncorrected lengths) and as computed on the assumption that the body-scale relationship takes the form of a parabola (corrected lengths). The lengths of the age groups at capture are designated by asterisks. All lengths are in millimeters.

[illegible]

crease and then to decrease. With the exception of age-group II the difference between the corrected and uncorrected calculated lengths always increased from the first to the second year of life. Beyond age-group III the differences tended to be approximately the same (within an age group) for the second and third years of life and to decrease progressively beyond the third year of life.

If the data of Table 8 are considered as a whole, it is apparent that the use of lengths calculated by direct proportion involves a high degree of error. For the earlier years of life, in particular, lengths calculated by direct proportion may give a seriously erroneous impression concerning the course of growth.

AVERAGE LENGTHS AND WEIGHTS OF THE AGE GROUPS

The average length (standard length in millimeters, total length in inches) and weight (in grams and ounces) of each age group (sexes separately) in each year's collection of the Nebish Lake rock bass are listed in Tables 9 and 10. The tables include also the grand average length and weight of each of the age groups for all collections combined.

TABLE 9. *Average length and weight of the age groups of male Nebish Lake rock bass in the different years of capture and for all years combined.*

Age group	Item	Year of capture				Grand average
		1930	1931	1932	1935	
XI	Standard length (millimeters)	..	..	195	..	195
	Weight (grams)	..	..	224	..	224
	Total length (inches)	..	..	9.3	..	9.3
	Weight (ounces)	..	..	7.9	..	7.9
	Number of fish	..	..	(3)	..	(3)
X	Standard length (millimeters)	..	190	188	171	187
	Weight (grams)	..	199	194	178	194
	Total length (inches)	..	9.1	9.0	8.2	9.0
	Weight (ounces)	..	7.0	6.8	6.3	6.8
	Number of fish	..	(4)	(10)	(1)	(15)
IX	Standard length (millimeters)	175	182	183	..	182
	Weight (grams)	161	179	180	..	179
	Total length (inches)	8.4	8.7	8.8	..	8.7
	Weight (ounces)	5.7	6.3	6.3	..	6.3
	Number of fish	(2)	(18)	(41)	..	(61)

TABLE 9 (continued)

Age group	Item	Year of capture				Grand average
		1930	1931	1932	1935	
VIII	Standard length (millimeters)	169	177	180	..	177
	Weight (grams)	141	164	167	..	164
	Total length (inches)	8.1	8.5	8.6	..	8.5
	Weight (ounces)	5.0	5.8	5.9	..	5.8
	Number of fish	(3)	(117)	(8)	..	(128)
VII	Standard length (millimeters)	166	177	174	..	173
	Weight (grams)	134	158	153	..	150
	Total length (inches)	8.0	8.5	8.3	..	8.3
	Weight (ounces)	4.7	5.6	5.4	..	5.3
	Number of fish	(15)	(27)	(5)	..	(47)
VI	Standard length (millimeters)	159	151	161	160	157
	Weight (grams)	114	99	120	150	120
	Total length (inches)	7.6	7.2	7.7	7.7	7.5
	Weight (ounces)	4.0	3.5	4.2	5.3	4.2
	Number of fish	(3)	(5)	(3)	(4)	(15)
V	Standard length (millimeters)	143	146	151	149	148
	Weight (grams)	84	93	98	116	104
	Total length (inches)	6.8	7.0	7.2	7.1	7.1
	Weight (ounces)	3.0	3.3	3.5	4.1	3.7
	Number of fish	(9)	(8)	(8)	(28)	(53)
IV	Standard length (millimeters)	125	135	146	128	133
	Weight (grams)	56	71	86	73	70
	Total length (inches)	6.0	6.5	7.0	6.1	6.4
	Weight (ounces)	2.0	2.5	3.0	2.6	2.5
	Number of fish	(9)	(3)	(7)	(5)	(24)
III	Standard length (millimeters)	..	116	121	..	120
	Weight (grams)	..	44	52	..	51
	Total length (inches)	..	5.6	5.8	..	5.7
	Weight (ounces)	..	1.6	1.8	..	1.8
	Number of fish	..	(6)	(43)	..	(49)
II	Standard length (millimeters)	..	89	93	..	93
	Weight (grams)	..	20	23	..	23
	Total length (inches)	..	4.3	4.5	..	4.5
	Weight (ounces)	..	0.7	0.8	..	0.8
	Number of fish	..	(10)	(78)	..	(88)

TABLE 10. Average length and weight of the age groups of female Nebish Lake rock bass in the different years of capture and for all years combined.

Age group	Item	Year of capture				Grand average
		1930	1931	1932	1935	
XIII	Standard length (millimeters)	..	..	193	..	193
	Weight (grams)	..	..	218	..	218
	Total length (inches)	..	..	9.2	..	9.2
	Weight (ounces)	..	..	7.7	..	7.7
	Number of fish	..	..	(1)	..	(1)
XII	Standard length (millimeters)	..	190	177	..	180
	Weight (grams)	..	210	167	..	178
	Total length (inches)	..	9.0	8.4	..	8.6
	Weight (ounces)	..	6.7	6.2	..	6.3
	Number of fish	..	(1)	(3)	..	(4)
XI	Standard length (millimeters)	..	182	180	177	180
	Weight (grams)	..	182	179	177	179
	Total length (inches)	..	8.6	8.6	8.4	8.6
	Weight (ounces)	..	6.4	6.3	6.2	6.3
	Number of fish	..	(2)	(13)	(1)	(16)
X	Standard length (millimeters)	154	176	175	..	175
	Weight (grams)	106	159	160	..	159
	Total length (inches)	7.4	8.4	8.3	..	8.3
	Weight (ounces)	3.7	5.6	5.6	..	5.6
	Number of fish	(1)	(17)	(33)	..	(51)
IX	Standard length (millimeters)	160	170	169	..	169
	Weight (grams)	125	149	144	..	146
	Total length (inches)	7.6	8.1	8.0	..	8.0
	Weight (ounces)	4.4	5.3	5.1	..	5.1
	Number of fish	(2)	(47)	(74)	..	(123)
VIII	Standard length (millimeters)	155	161	164	170	161
	Weight (grams)	113	124	129	174	124
	Total length (inches)	7.4	7.6	7.8	8.1	7.6
	Weight (ounces)	4.0	4.4	4.6	6.1	4.4
	Number of fish	(8)	(99)	(17)	(1)	(125)
VII	Standard length (millimeters)	149	159	159	..	153
	Weight (grams)	97	119	119	..	107
	Total length (inches)	7.1	7.6	7.6	..	7.3
	Weight (ounces)	3.4	4.2	4.2	..	3.8
	Number of fish	(43)	(24)	(9)	..	(76)
VI	Standard length (millimeters)	145	149	149	155	150
	Weight (grams)	88	96	96	129	103
	Total length (inches)	6.9	7.1	7.1	7.4	7.2
	Weight (ounces)	3.1	3.4	3.4	4.6	3.6
	Number of fish	(6)	(11)	(8)	(9)	(34)

TABLE 10 (continued)

Age group	Item	Year of capture				Grand average
		1930	1931	1932	1935	
V	Standard length (millimeters)	127	135	142	140	138
	Weight (grams)	62	74	82	96	89
	Total length (inches)	6.1	6.5	6.8	6.7	6.6
	Weight (ounces)	2.2	2.6	2.9	3.4	3.1
	Number of fish	(6)	(7)	(2)	(43)	(58)
IV	Standard length (millimeters)	118	125	137	130	128
	Weight (grams)	47	58	73	78	64
	Total length (inches)	5.7	6.0	6.6	6.2	6.1
	Weight (ounces)	1.7	2.0	2.6	2.8	2.3
	Number of fish	(9)	(5)	(9)	(8)	(31)
III	Standard length (millimeters)	..	112	114	111	114
	Weight (grams)	..	40	43	51	43
	Total length (inches)	..	5.4	5.5	5.3	5.5
	Weight (ounces)	..	1.4	1.5	1.8	1.5
	Number of fish	..	(7)	(59)	(1)	(67)
II	Standard length (millimeters)	..	89	90	..	90
	Weight (grams)	..	21	21	..	21
	Total length (inches)	..	4.3	4.3	..	4.3
	Weight (ounces)	..	0.7	0.7	..	0.7
	Number of fish	..	(9)	(59)	..	(68)

The agreement as to average length and weight of rock bass of the same age and sex but taken in different years is in general good. Some of the discrepancies that do occur are doubtless the result of the small numbers of fish in certain age groups. Others are traceable to differences in growth rate in different calendar years.¹⁸ The high average weights of the age groups in the 1935 collection depend on the extremely good condition of the rock bass in late August of that year.

In spite of the general similarity of the size of fish of the same age and sex but taken in different years, there is nevertheless a noticeable tendency for the average lengths and weights of the age groups to increase from year to year over the period, 1930 to 1932. All ages below the VI-group follow this trend closely. Although the same general upward trend is detectable among the older fish, the data for the VI and older groups contain a number of exceptions. The observed upward trend in the average size of the age groups may be connected with the im-

¹⁸ The question of annual fluctuations in growth is treated in detail in a later section (pp. 249 to 262).

provement that was occurring in the growth rate of the rock bass in 1930 and 1931.

Rock bass captured in 1935 usually were shorter but heavier than fish of the same age and sex in 1932. The only exceptions in age groups represented by more than one fish were the VI-group females which were 6 millimeters longer in 1935 and the IV-group males which were not only 18 millimeters shorter but also 13 grams lighter in 1935 than in 1932. The reason for the high weights of the 1935 age groups was mentioned two paragraphs previously. Their decreased length in comparison with 1932 age groups was correlated with a decline in growth rate in the years, 1932 to 1934 (p. 258).

The slow growth of the Nebish Lake rock bass prevents the attainment of a large size despite the fact that many of them survive to the age of 9 years or older. The age group with the greatest average size, the XI-group males of the 1932 collection, had an average length¹⁹ of only 195 millimeters (9.3 inches) and an average weight of only 224 grams (7.9 ounces). Among the males no age group younger than the X-group had an average length as great as 187 millimeters (9 inches) and all age groups younger than the VII-group averaged less than 166 millimeters (8 inches). The small size attained by the females is even more striking. The grand average length of IX-group female rock bass was only 169 millimeters (8 inches) and no age group represented by more than one fish had a grand average length in excess of 180 millimeters (8.6 inches) or a grand average weight above 179 grams (6.3 ounces).

Data concerning the maximum average length and weight attained by age groups ordinarily do not provide information as to the maximum size attained by individual fish. It happens that the XIII-group female captured in 1932 not only was the oldest fish of that sex in the collections but also was the longest (193 millimeters, 9.2 inches) and the heaviest (218 grams, 7.7 ounces). However, males were captured whose size was greater than the average for any age group. The longest males taken were three 200-millimeter (9.6 inches) fish in the 1932 collection. One of these fish was also the heaviest (257 grams or 9.1

¹⁹ In this and later discussions all lengths given in millimeters are standard and those given in inches are total.

ounces). The age of this individual could not be determined. Of the remaining 200-millimeter male rock bass one was a member of age-group XI and weighed 253 grams (8.9 ounces) and the other of age-group X and weighed 242 grams (8.5 ounces).

The grand average lengths for the age groups show that males ordinarily attain the minimum legal length of 7 inches in the sixth year of life (age-group V) and females in the seventh (age-group VI). The averages for the age groups in the collections for the individual years indicate that with good or poor growth the age at which legal length is attained may be subject to some annual variation.

In order not to disturb the continuity of the preceding discussions, the standard and total lengths of rock bass have been presented without a statement of the relationship between the two measurements or of the conversion factors employed. Table 11 contains factors for conversions between standard and total length, as determined from measurements of 306 rock bass captured in 1930. The most noteworthy conclusions to be drawn from the data are: (1) small rock bass have relatively longer tails than large ones; and (2) among the largest rock bass the males have longer tails than the females. The observation as to the decrease in the relative length of the caudal fin with increase in body length is in agreement with the findings of Van Oosten on the Lake Erie sheepshead (1938), and the Lake Huron whitefish (1939).

TABLE 11. *Factors for conversions between total length (T.L.) and standard length (S.L.) of rock bass according to sex and length group.*

Sex	Standard length interval	Number of fish	Factors for conversion of			
			T.L. to S.L. (No change of unit)	S.L. to T.L. (No change of unit)	T.L. (inches) to S.L. (millimeters)	S.L. (millimeters) to T.L. (inches)
Both	Less than 100 millimeters	29	0.818	1.222	20.78	0.0481
Male	100 millimeters or greater	136	0.822	1.217	20.88	0.0479
Female	100-159 millimeters	109				
Female	160 millimeters or greater	32	0.829	1.206	21.06	0.0475

RANGE OF LENGTH IN THE AGE GROUPS

The length-frequency distributions of the age groups of the Nebish Lake rock bass (Tables 12 and 13) have been based on the combination of the data for fish of corresponding age and

TABLE 12. *Length-frequency distributions of the age groups of the male rock bass of Nebish Lake.*

Length interval in millimeters	Age group										Total
	II	III	IV	V	VI	VII	VIII	IX	X	XI	
200-204	..	..	..	..	..	..	..	..	1	1	2
195-199	..	..	..	..	..	..	1	1	1	..	3
190-194	..	..	..	..	..	..	..	5	4	2	11
185-189	..	..	..	..	..	2	13	18	5	..	38
180-184	..	..	..	..	..	5	40	18	1	..	64
175-179	..	..	..	..	..	11	29	12	3	..	55
170-174	..	..	..	..	..	18	35	7	..	..	60
165-169	..	..	..	..	1	4	8	..	..	..	13
160-164	..	..	..	1	7	5	1	..	..	..	14
155-159	..	..	..	8	3	1	..	..	..	..	12
150-154	..	..	1	17	2	1	1	..	..	..	22
145-149	..	..	2	11	1	..	..	..	..	..	14
140-144	..	..	5	9	1	..	..	..	..	..	15
135-139	..	2	1	3	..	..	..	..	..	..	6
130-134	..	5	2	4	..	..	..	..	..	..	11
125-129	..	5	3	..	..	..	..	..	..	..	8
120-124	..	15	1	..	..	..	..	..	..	..	16
115-119	..	8	..	..	..	..	..	..	..	..	8
110-114	1	5	..	..	..	..	..	..	..	..	6
105-109	4	1	..	..	..	..	..	..	..	..	5
100-104	12	2	..	..	..	..	..	..	..	..	14
95- 99	9	..	..	..	..	..	..	..	..	..	9
90- 94	23	..	..	..	..	..	..	..	..	..	23
85- 89	24	..	..	..	..	..	..	..	..	..	24
80- 84	5	..	..	..	..	..	..	..	..	..	5
Average length	93	121	138	148	157	173	177	182	187	195	..
Number of fish	78	43	15	53	15	47	128	61	15	3	458

sex in the different years' collections, with the exception of those age groups for which records of sex were incomplete or lacking. The age groups that were excluded in the preparation of the tables were: II- and III-groups of 1930 and 1931; IV-group of 1930.

The data of Tables 12 and 13 give no evidence that the length range of an age group varies according to the age or sex of the fish involved. Among the 15 age groups that were represented by more than 20 fish the length range varied from 25 millimeters (II-group females) to 50 millimeters (VIII-group males). Ten of the 15 age groups had length ranges of 35 or 40 millimeters.

The generally high degree of overlap of the length-frequency distributions of the successive age groups of both sexes makes length a relatively poor index of age. The positions of the modal lengths of only the II-groups stand out distinctly in the length-frequency distributions for all ages combined. Larger rock bass at any particular length may belong to any one of several age groups. Among the males as many as five age groups were rep-

Among the females whose slower growth led to a greater overlap of the length-frequency distributions of the successive age groups, six age groups were represented in the intervals, 150-154 millimeters and 165-169 millimeters.

CALCULATED LENGTHS OF THE AGE GROUPS AND THE YEAR CLASSES

The calculated growth histories of the individual age groups in each year's collection of the Nebish Lake rock bass are recorded in Tables 14, 15, and 16. In the general arrangement of the data, fish of the same year class rather than of the same age have been grouped together. The data on the younger fish for which there were no sex records (Table 16) have been included largely for the sake of completeness, since the lack of these records renders the data of small value in the analysis of growth. The growth histories of the individual year classes, all ages combined, are presented in Tables 17 and 18.

The present section will be concerned only with variations in calculated lengths, and will not include the consideration of

TABLE 13. *Length-frequency distributions of the age groups of female rock bass of Nebish Lake.*

Length interval in millimeters	Age group												Total
	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	
190-194	..	..	..	..	..	..	..	2	..	..	1	1	4
185-189	..	..	..	..	..	..	..	..	1	2	..	..	3
180-184	..	..	..	..	..	..	..	2	8	8	1	..	19
175-179	..	..	..	..	..	..	2	22	20	5	1	..	50
170-174	..	..	..	..	..	2	18	40	17	..	1	..	78
165-169	..	..	..	..	1	4	16	27	4	1	..	..	53
160-164	..	..	..	..	1	11	38	21	..	..	..	..	71
155-159	..	..	..	..	5	17	27	6	..	..	..	..	55
150-154	..	..	..	2	10	20	21	3	1	..	..	..	57
145-149	..	..	2	10	12	12	2	..	..	..	..	..	38
140-144	..	..	2	14	4	9	1	..	..	..	..	..	30
135-139	..	..	4	15	1	1	..	..	..	..	..	..	21
130-134	..	..	4	12	..	..	..	..	..	..	..	..	16
125-129	..	2	5	2	..	..	..	..	..	..	..	..	9
120-124	..	9	5	2	..	..	..	..	..	..	..	..	16
115-119	..	19	..	1	..	..	..	..	..	..	..	..	20
110-114	..	17	..	..	..	..	..	..	..	..	..	..	17
105-109	..	6	..	..	..	..	..	..	..	..	..	..	6
100-104	6	5	..	..	..	..	..	..	..	..	..	..	11
95- 99	3	2	..	..	..	..	..	..	..	..	..	..	5
90- 94	21	..	..	..	..	..	..	..	..	..	..	..	21
85- 89	22	..	..	..	..	..	..	..	..	..	..	..	22
80- 84	7	..	..	..	..	..	..	..	..	..	..	..	7
Average length	90	114	132	138	150	153	161	169	175	180	180	193	..
Number of fish	59	60	22	58	34	76	125	123	51	16	4	1	629

TABLE 14. Average length in millimeters at capture and average calculated length at the end of each year of life for each age group of male Nebish Lake rock bass, arranged by year class and year of capture. Below, general growth data based on all age groups except the II-groups (designated by asterisks).

Year class	Year of capture	Age group	Number of fish	Length at capture	Calculated length at end of year of life										
					1	2	3	4	5	6	7	8	9	10	11
1921	{ 1930	IX	2	175	44	73	101	125	142	155	162	168	172	186	..
	{ 1931	X	4	190	35	66	102	127	145	156	168	174	180	183	..
	{ 1932	XI	3	195	38	72	101	123	143	157	167	173	178	183	190
1922	{ 1930	VIII	3	169	37	65	93	118	139	152	161	166	..	..	..
	{ 1931	IX	18	182	39	70	98	120	141	157	165	172	178	..	..
	{ 1932	X	10	188	40	73	99	123	145	159	167	172	177	184	..
1923	{ 1930	VII	15	166	35	64	93	116	138	152	160	..	..	..	..
	{ 1931	VIII	117	177	37	63	93	120	140	153	164	172	..	..	..
	{ 1932	IX	41	183	36	63	94	121	141	153	163	171	179	..	..
1924	{ 1930	VI	3	159	34	61	86	114	133	151	..	..	..	..	..
	{ 1931	VII	27	177	40	72	102	129	149	162	172	..	..	..	..
	{ 1932	VIII	8	180	40	69	99	125	147	159	168	175	..	..	..
1925	{ 1930	V	9	143	34	57	83	107	128	..	..	..	..	..	..
	{ 1931	VI	5	151	30	50	74	100	124	141	..	..	..	..	..
	{ 1932	VII	5	174	35	60	88	112	136	154	170	..	..	..	..
1926	{ 1935	X	1	171	35	65	82	107	128	141	149	157	164	171	..
	{ 1930	IV	9	125	29	51	73	105	..	..	..	..	..	..	..
	{ 1931	V	8	146	29	50	73	102	125	..	..	..	..	..	..
1927	{ 1932	VI	3	161	37	62	88	114	132	151	..	..	..	..	..
	{ 1931	IV	3	135	30	54	82	112	..	..	..	..	..	..	..
	{ 1932	V	8	151	28	50	79	106	134	..	..	..	..	..	..
1928	{ 1931	III	6	116	32	61	92	122	..	..	..	..	..	..	..
	{ 1932	IV	7	146	30	56	89	..	..	..	..	..	..	..	..
1929	{ 1931	II*	10	89	31	63	..	..	..	..	..	..	..	..	..
	{ 1932	III	43	121	29	61	95	..	..	..	..	..	..	..	..
	{ 1935	VI	4	160	27	55	87	120	141	153	..	..	..	..	..
1930	{ 1932	II*	78	93	34	65	..	..	..	..	..	..	..	..	..
	{ 1935	V	28	149	31	59	89	117	137	..	..	..	..	..	..
	{ 1935	IV	5	128	29	55	81	103	..	..	..	..	..	..	..
Average calculated length					35	62	92	119	139	153	163	171	177	184	191
Average growth increment					34.8	27.6	29.8	26.6	20.6	13.4	10.2	7.6	6.8	6.3	7.0
Number of fish					(395)	(395)	(395)	(346)	(322)	(269)	(254)	(207)	(79)	(18)	(3)

increments of growth in length or of annual fluctuations in growth rate. The detailed study of annual fluctuations in growth rate as determined from the analysis of the growth increments of the various year classes will be presented in a later section (pp. 249-262).

The calculated lengths of the age groups give little or no indication of the presence of Lee's phenomenon of apparent decrease in calculated length as it is determined from successively older groups of fish (Tables 14 and 15). In fact, the calculated lengths for the early years of life were usually greater among the older age groups (VI- or VII-group and older) than in the younger (III to V or VI). It is true that in some of the year classes represented by the age-groups III to VI the older fish had slightly lower calculated lengths than younger fish of the same year class. (The II-group probably was not represented adequately—see p. 197.) However, these discrepancies were usually small and did not occur consistently in all the year classes. Furthermore, the majority of the age groups involved contained only small numbers of specimens. The disagreements can not, therefore, safely be considered to represent Lee's phenomenon. Consequently, the general conclusion that Lee's phenomenon, if present at all, has no significant effect on the determination of calculated growths of the Nebish Lake rock bass appears to be justified.

The disagreements that occur among the calculated lengths of different age groups of the same year class can be attributed for the most part to the small numbers of specimens in the individual age groups. Gear selectivity may have played a rôle also. Usually, however, the agreement is good where the numbers of fish are large.

The differences between the calculated lengths of the age groups of a single year class are usually much less than the differences to be found between age groups of different year classes. As an illustration, the maximum difference²⁰ of 5 millimeters in the first-year length of female rock bass within a year class (year class of 1921) is much less than the 13-millimeter difference between the first-year lengths of the 1930 IX-group

²⁰ Age groups represented by only one fish have been disregarded in determination of the maximum discrepancies of calculated growth.

TABLE 15. Average length in millimeters at capture and average calculated length at the end of each year of life for each age group of female Nebish Lake rock bass, arranged by year class and year of capture. Below, general growth data based on all age groups except the II-groups (designated by asterisks).

Year class	Year of capture	Age group	Number of fish	Length at capture	Calculated length at end of year of life												
					1	2	3	4	5	6	7	8	9	10	11	12	13
1919	{ 1931 1932	XII XIII	1 1	190 193	40 40	76 68	115 107	147 141	160 158	165 163	169 166	173 170	177 175	182 177	185 180	187 185	.. 192
1920	{ 1930 1931 1932	X XI XII	1 2 3	154 182 177	32 33 32	68 60 57	102 92 86	124 125 113	131 140 132	138 150 140	142 157 146	148 163 152	151 171 159	153 171 164	.. 178 168	.. 175	..
1921	{ 1930 1931 1932	IX X XI	2 17 13	160 176 180	41 36 36	67 70 66	94 100 97	117 121 118	130 136 135	139 147 146	149 155 154	154 161 159	158 167 164	.. 170 159	.. 177	..	..
1922	{ 1930 1931 1932	VIII IX X	8 47 33	155 170 175	35 35 38	69 65 72	90 94 100	109 116 120	129 134 137	141 146 148	147 154 155	152 160 161	.. 165 166	.. 173	..	..	..
1923	{ 1930 1931 1932	VII VIII IX	43 99 74	149 161 169	34 36 36	58 63 62	86 90 91	109 113 114	126 130 131	136 141 142	145 149 151	.. 156 157	.. 165	..	..	..	..
1924	{ 1930 1931 1932 1935	VI VII VIII XI	6 24 17 1	145 159 164 177	34 36 38 32	60 65 70 53	86 93 96 88	110 116 116 114	127 132 134 132	139 144 147 143	.. 153 153 151	.. 160 158	 168	 173	..	..	..
1925	{ 1930 1931 1932	V VI VII	6 11 9	127 149 159	34 35 37	54 60 61	75 84 87	95 107 108	114 126 128	.. 140 141	 153			..	..	..	..
1926	{ 1930 1931 1932	IV V VI	9 7 8	118 135 149	29 31 29	52 54 52	73 71 74	98 94 100	.. 116 120	 140				..	..	..	..
1927	{ 1931 1932 1935	IV V VIII	5 2 1	125 142 170	29 32 28	49 55 56	73 80 78	100 104 102	.. 126 121	 143	 154	 160		..	..	..	..
1928	{ 1931 1932	III IV	7 9	112 137	31 30	55 54	87 84	.. 114	..	..	..	..	..	..	..	..	..
1929	{ 1931 1932 1935	II* III VI	9 59 9	89 114 155	32 29 29	64 59 57	.. 89 88	 115	..	..	..	..	..	..	..	..	..
1930	{ 1932 1935	II* V	59 43	90 140	33 29	64 57	.. 86	.. 111	..	..	..	..	..	..	..	..	..
1931	1935	IV	8	130	28	55	84	109	..	..	..	..	..	..	..	..	..
1932	1935	III	1	111	27	52	83	..	..	..	..	..	..	..	..	..	..
Average calculated length				..	34	62	90	113	130	142	150	156	162	168	174	179	186
Average growth increment				..	33.9	27.8	27.9	23.0	17.5	11.4	8.2	6.3	6.3	5.3	6.2	5.6	7.0
Number of fish				..	(586)	(586)	(586)	(519)	(488)	(430)	(396)	(320)	(195)	(72)	(21)	(5)	(1)

and the 1935 IV-group. Similarly the 10-millimeter discrepancy in the second-year lengths of the 1924 year class is less than the difference of 23 millimeters between the second-year lengths of the 1932 X-group and the 1931 IV-group. A like relationship holds for the calculated lengths for other years of life and for the calculated growth data for the males. The comparison of the growth histories of the age groups (Tables 14 and 15) with the average growth of the year classes (Tables 17 and 18) reveals that the relatively limited variation of calculated lengths within a year class is the result of a strong tendency for each age group to conform to the "style of growth" that is typical for the year class to which it belongs.

TABLE 16. *Average length in millimeters at capture and average calculated length at the end of each year of life for each age group of young Nebish Lake rock bass, based on fish for which there are no sex records.*

Year class	Year of capture	Age group	Number of fish	Length at capture	Calculated length at end of year of life			
					1	2	3	4
1926	1930	IV	6	118	28	53	74	99
1927	1930	III	9	99	26	50	75	..
1928	1930	II	21	80	28	54	..	..
	1931	III	1	118	28	56	92	..
1929	1931	II	41	85	32	61	..	..

TABLE 17. *Calculated length in millimeters at the end of each year of life of the males of each year class of the Nebish Lake rock bass.*

Year class	Number of fish	Calculated length at end of year of life										
		1	2	3	4	5	6	7	8	9	10	11
1921	9	38	70	101	125	144	156	166	172	178	184	191
1922	31	39	70	98	121	142	157	165	171	177	184	...
1923	173	37	63	93	120	140	153	163	171	179	...	...
1924	38	40	70	100	127	147	160	170	177	...	...	...
1925	20	33	56	82	106	129	146	161	¹ 169	¹ 176	¹ 181	...
1926	20	30	52	75	105	127	146	...	...	...	...	...
1927	11	29	51	80	108	136	...	...	...	...	...	...
1928	13	31	58	90	123	...	...	...	...	...	...	...
1929	47	29	60	94	¹ 127	¹ 148	¹ 160	...	...	...	...	...
1930	28	31	59	89	117	137	...	...	...	...	...	...
1931	5	29	55	81	103	...	...	...	...	...	...	...
Maximum difference		11	19	26	24	20	14	9	6	2	0	...
Maximum difference as percentage of lowest calculated length		37.9	37.2	34.7	23.3	15.7	9.6	5.6	3.5	1.1	0.0	...

¹ Calculated length excluded from the computation of the maximum difference because of inadequate representation.

TABLE 18. *Calculated length in millimeters at the end of each year of life of the females of each year class of the Nebish Lake rock bass.*

Year class	Number of fish	Calculated length at end of year of life												
		1	2	3	4	5	6	7	8	9	10	11	12	13
¹ 1919	2	40	72	111	144	159	164	168	172	176	180	183	186	193
1920	6	32	60	91	119	134	143	149	155	162	166	170	177	..
1921	32	36	68	98	120	135	146	154	160	165	169	177	..	..
1922	88	36	68	96	117	135	146	154	160	165	172	..	..	..
1923	216	36	62	90	113	130	141	149	156	164	..	..	..	..
1924	48	36	66	93	115	132	144	152	159	¹ 169	¹ 174	¹ 177	..	..
1925	26	35	59	83	105	124	138	150	..	..	..	..	..	..
1926	24	30	53	73	98	119	139	..	..	..	..	..	..	..
1927	8	30	51	75	101	122	144	¹ 155	¹ 161	..	..	..	..	..
1928	16	30	54	85	115	..	..	..	..	..	..	..	..	..
1929	68	29	59	89	116	138	150	..	..	..	..	..	..	..
1930	43	29	57	86	111	129	..	..	..	..	..	..	..	..
1931	8	28	55	84	109	..	..	..	..	..	..	..	..	..
¹ 1932	1	27	52	83	..	..	..	..	..	..	..	..	..	..
Maximum difference		8	17	25	22	19	12	5	5	3	6	7	..	..
Maximum difference as percentage of lowest calculated length		28.6	33.3	34.2	22.4	16.0	8.7	3.4	3.2	1.9	3.6	4.1	..	..

¹ Year class or individual calculated length excluded from the computation of maximum difference because of inadequate representation.

The great extent to which the growth histories of the year classes may differ is brought out by the data of Tables 17 and 18. (See Figures 5 and 6.) These differences in the manner of growth led to a wide range of variation among the year classes in the relationship of length to age, particularly in the earlier years of life. In both sexes the differences between the largest and smallest calculated lengths of year classes at corresponding ages (maximum difference) increased rapidly from the first to the third year of life. Beyond the third year the maximum differences decreased continuously for the males and over a period of several years for the females. The data for the later years of life of the females were irregular. The relative advantages of the largest over the smallest calculated lengths at corresponding years of life (maximum differences as percentage of lowest calculated length) were much the same during the first three years. Beyond the third year the percentages as well as the absolute differences underwent a pronounced decline (continuous for the males and irregular for the females).

Differences in the growth of year classes may lead also to variations in different calendar years in the relationship of length to age. The light broken lines of Figures 5 and 6 that connect the calculated lengths for corresponding years of life

show, for example, that rock bass were smaller at most ages in 1929 than in the preceding and subsequent calendar years. In other years, as for example in 1924, the Nebish Lake rock bass were relatively large for their age.

The growth of both the males and females of the 1924 year class introduces irregularities into the general trend of the data on the fluctuations in the relationship of size to age in different calendar years. From Tables 17 and 18 and Figures 5 and 6, it may be seen that in some years, especially in 1926, 1927, and 1928, the calculated lengths as a whole tended to be smaller than those for fish in corresponding years of life in the calendar year immediately preceding. However, the regularity with which the calculated lengths of rock bass of the 1924 year class exceeded those of the 1923 year class introduced a series of exceptions to the general trend. At first these discrepancies suggested the

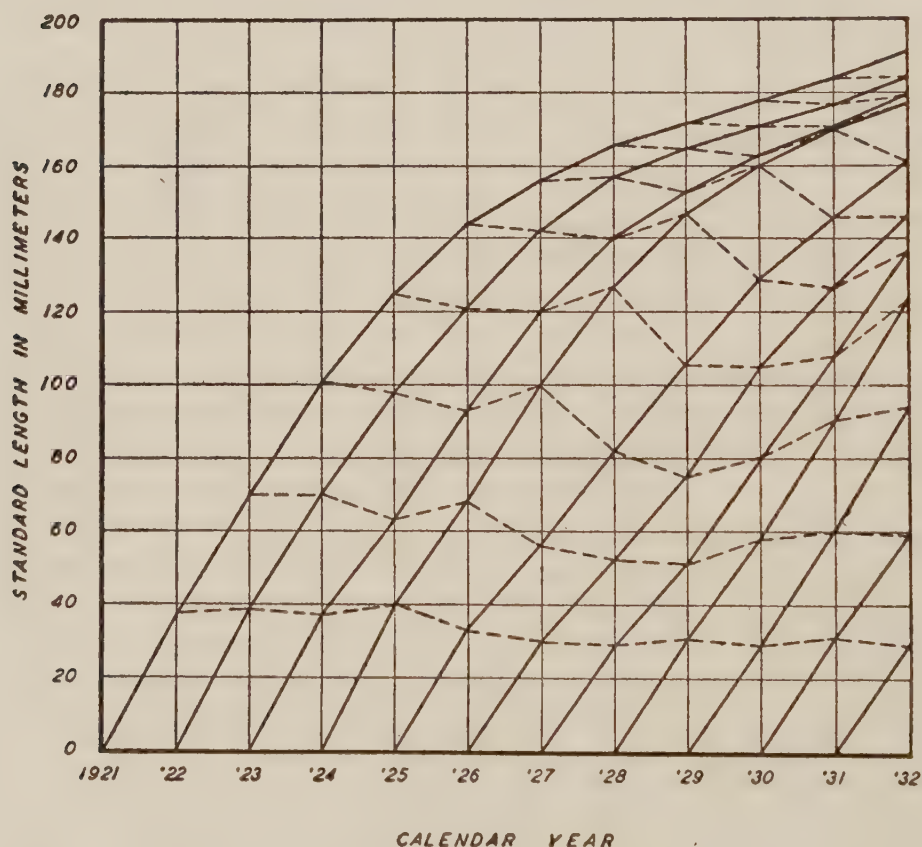


FIGURE 5. Calculated growth histories of the year classes of male Nebish Lake rock bass. The calculated lengths for corresponding years of life in different calendar years have been connected by light lines.

rather unpleasant possibility that erroneous age determinations of 1923 year-class fish (the overlooking of one annulus) might account for the large average calculated lengths of the 1924 year class. The 1923 year class was so very abundant that errors in the age determination of even a small percentage of them might well produce a serious distortion of the data for the much weaker 1924 year class.

There are strong arguments, however, against the belief that the high calculated lengths of the 1924 year class are the result of the erroneous inclusion of individuals of the 1923 year class. The discrepancies are not confined to the later years of life where the annuli may be difficult to detect, but occur also in the calculated lengths of the early years. The detection of the first five or six annuli is almost always a very simple matter. Consequently it appears that the 1923 and 1924 year classes exhibit differences in growth that can not well be attributed to errors in scale reading.

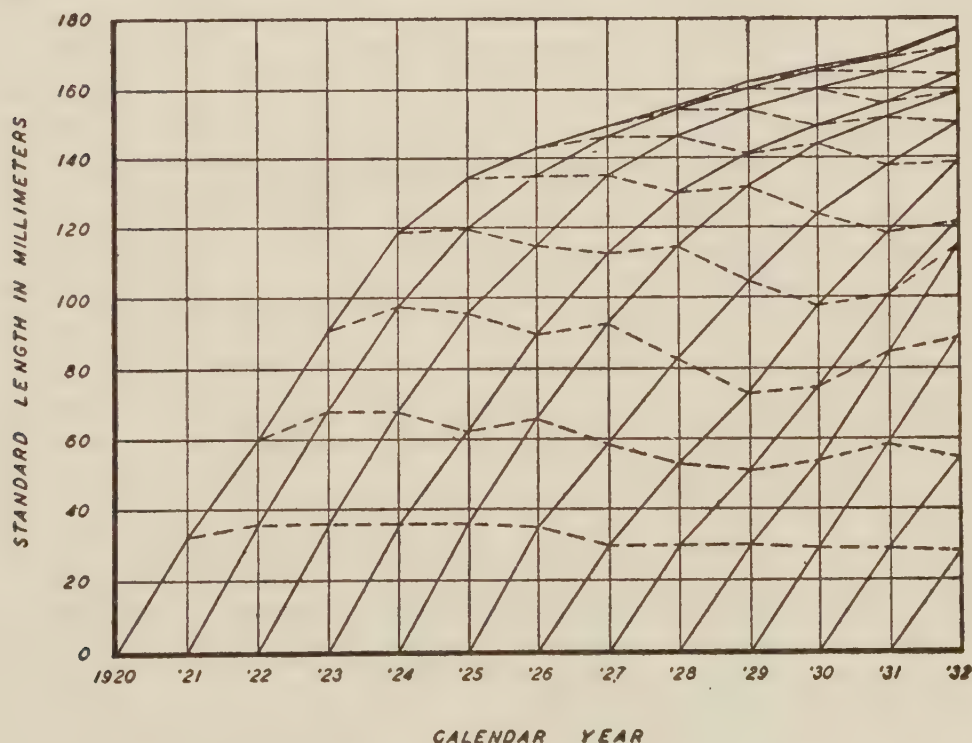


FIGURE 6. Calculated growth histories of the year classes of female Nebish Lake rock bass. The calculated lengths for corresponding years of life in different calendar years have been connected by light lines. Compare with Fig. 5.

TABLE 19. Average calculated length at end of each year of life, annual increment of growth in length, and annual percentage increase in length of the Nebish Lake rock bass, all collections combined. The average calculated lengths are based on summations of the average increments of growth in length.

Males						Females					
Number of fish	Year of life	Length in millimeters	ΔL	$\frac{100\Delta L}{L}$	Number of fish	Year of life	Length in millimeters	ΔL	$\frac{100\Delta L}{L}$	Ratio of increments of sexes	Difference between increments of sexes
..	..	..	..	..	1	13	186	7.0	3.9	..	..
..	..	..	..	..	5	12	179	5.6	3.2	..	..
3	11	191	7.0	3.8	21	11	174	6.2	3.7	1.13	0.8
18	10	184	6.3	3.6	72	10	168	5.3	3.3	1.19	1.0
79	9	177	6.8	4.0	195	9	162	6.3	4.0	1.08	0.5
207	8	171	7.6	4.7	320	8	156	6.3	4.2	1.21	1.3
254	7	163	10.2	6.7	396	7	150	8.2	5.8	1.24	2.0
269	6	153	13.4	9.6	430	6	142	11.4	8.3	1.18	2.0
322	5	139	20.6	17.3	488	5	130	17.5	15.5	1.18	3.1
346	4	119	26.6	28.9	519	4	113	23.0	25.6	1.16	3.6
395	3	92	29.8	48.1	586	3	90	27.9	45.0	1.07	1.9
395	2	62	27.6	78.9	586	2	62	27.8	81.8	0.99	-0.2
395	1	35	34.8	..	586	1	34	33.9	..	1.03	0.9

With fish of such advanced age some errors in age determination almost certainly occurred. However, the rejection of all highly questionable scales must have minimized the possible effects of these errors. Although inaccurate scale readings may have contributed to the discrepancies between the calculated lengths of the 1923 and 1924 year classes, it is not believed that the observed differences are entirely the result of such errors.

GENERAL GROWTH

GROWTH IN LENGTH

The calculated lengths of all collections have been combined²¹ to determine general curves of growth in length for the Nebish Lake rock bass (Table 19, Figs. 7, 8, and 9). The lengths of Table 19 are not the grand averages of the calculated lengths, but are rather the successive summations of the grand average increments (ΔL) of calculated growth in length. The use of grand average increments yields a smoother curve and one more in conformity with the actual data on growth in different years of life.

The data of Table 19 and Figures 7, 8, and 9 are general in the sense that they have been derived from all the reliable materials available. Information already presented on variations of growth among year classes (p. 229) and data to be presented later (p. 249) on annual fluctuations in growth rate are sufficient to prove that rock bass taken in another period of calendar years almost certainly would have yielded a slightly different general growth curve. The present general growth data must be recognized, therefore, as only roughly descriptive of the true typical growth, if indeed a clearly defined general growth curve can be said to exist at all.

The growth curves for the sexes have the same general form. The males nevertheless grow at a distinctly higher rate. The divergence of the growth curves for the sexes (Fig. 7) begins at the third year of life but is not distinctly noticeable until the fourth. The advantage of the males becomes more apparent in the light of comparisons as to the number of years required to

²¹ All II-group fish were excluded from the computations of general growth (p. 197).

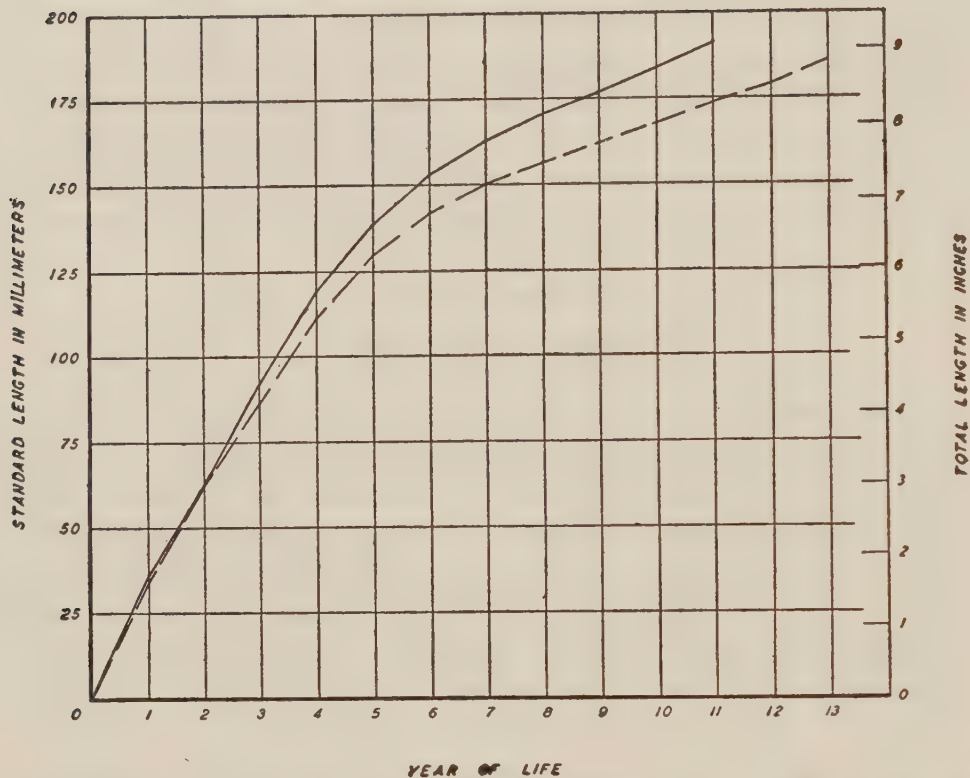


FIGURE 7. Grand average calculated length of the Nebish Lake rock bass at the end of each year of life. Solid line males, broken line females.

attain certain lengths. For example, males were 3 millimeters longer at the end of 6 years than females at the end of 7. At the end of 7 years of life the length of the males was 1 millimeter above the ninth-year length of females. In fact, at all ages beyond the sixth year, males were consistently longer than females that were 2 years older.

The ratios of the increments of the sexes and the differences between the increments (at extreme right at Table 19) show the relative and actual advantages of the growth of the males in different years of life. The greatest actual advantage of the males occurred in the fourth year (3.6 millimeters)—(See also, Fig. 8), but the relative advantage at that time was less than in all but two of the later years of life. The greatest relative advantage in the growth of the males was in the seventh year when the length increment of the males was 1.24 times that of the females.

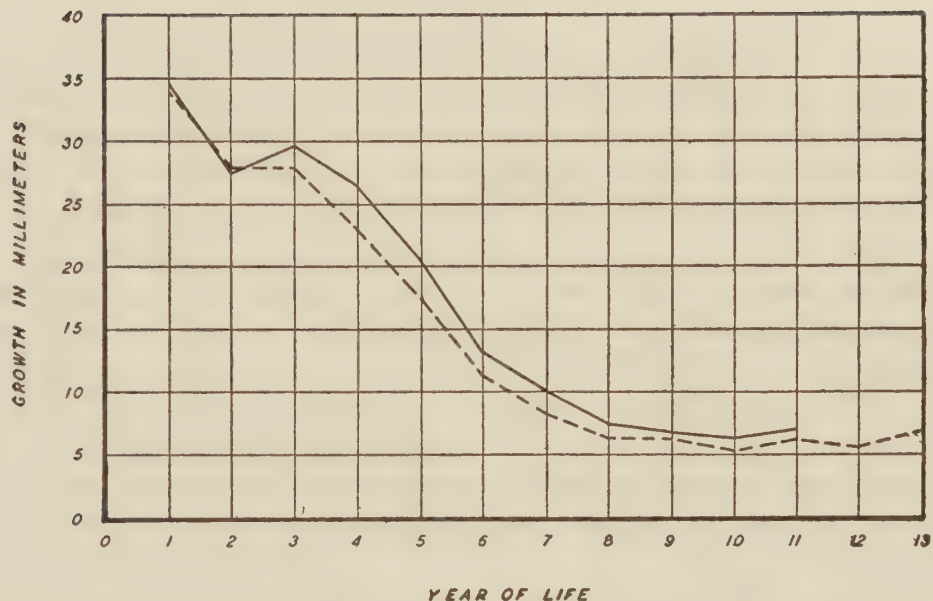


FIGURE 8. Calculated increments of the growth in length of the Nebish Lake rock bass in each year of life. Solid line males, broken line females.

The growth of each sex in the first year was greater than in any other year of life. The length increment decreased in the second year and increased in the third. In the males this increase was sufficient to give the growth curve a definite inflection, but in the females it was too small to have any significance. The annual increments of growth in length of both sexes decreased continuously from the fourth to the eleventh year. (The equal eighth- and ninth-year increments of the females provide a single exception.) Both sexes showed improved growth in the eleventh year (only three male specimens). Only females were represented beyond the eleventh year; the increments of the twelfth and thirteenth years of life gave no indication of any pronounced further change in growth.

The rate of growth, as expressed by the annual percentage $\left(\frac{100\Delta L}{L}\right)$ increase (Fig. 9) declined continuously from the second to the eleventh year of life. The decrease was rapid in the earlier years. The annual percentage increase did not exceed 10 per cent beyond the fifth year in either sex, or 4 per cent beyond the eighth.

GROWTH IN WEIGHT

The data on general growth in weight (Table 20 and Fig. 10) correspond exactly with the data on general growth in length (Table 19); that is, the weights of Table 20 have been computed from the calculated lengths at the end of each year of life. The length-weight equation from which the computations were made is discussed on p. 311. The same equation was employed in the computations for both sexes. The positions of the empirical grand averages²² for the age groups with respect to the computed curves of growth in weight also are indicated in Figure 10. (The lack of information on the length of males at the end of the twelfth year and of the females at the end of the fourteenth year makes impossible the determination of the positions of the points for the XI-group males and the XIII-group females.)

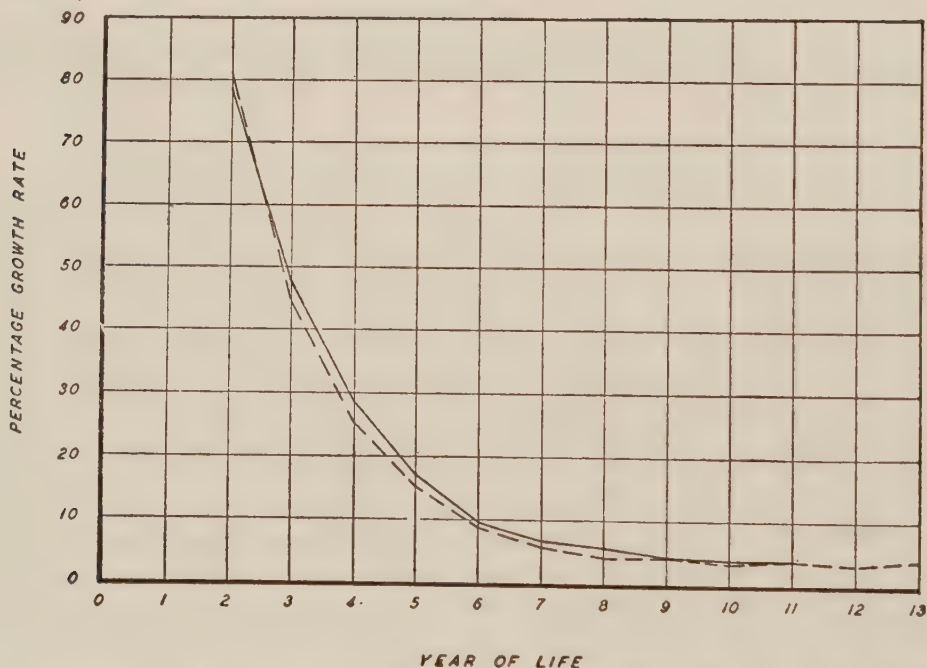


FIGURE 9. Percentage increase in the calculated length of the Nebish Lake rock bass in each year of life. Solid line males, broken line females.

²² The average weights of the age groups of the 1935 collection were not included in the empirical grand averages because of the disagreement of the length-weight relationship in 1935 with that of earlier years (p. 307). The grand average empirical weights for age groups that were represented in the 1935 collection were computed from the grand average empirical lengths (including the 1935 samples) and the grand average value of the coefficient of condition, K , for the collections of 1930, 1931, and 1932 (Table 58).

TABLE 20. Calculated weight at the end of each year of life, annual increment of growth in weight, and annual percentage increase in weight of the Nebish Lake rock bass. The weights which correspond to the lengths of Table 19 were calculated from the equation, $\log W = -4.54002175 + 3.003 \log L$.

Males						Females					
Number of fish	Year of life	Weight in grams	ΔW	$\frac{100\Delta W}{W}$	Number of fish	Year of life	Weight in grams	ΔW	$\frac{100\Delta W}{W}$	Ratio of increments of sexes	Difference between increments of sexes
..	..	..	..	..	1	13	189	21	12.5	...	..
..	..	..	..	..	5	12	168	14	9.1	...	..
3	11	204	22	12.1	21	11	154	15	10.8	1.47	7
18	10	182	20	12.3	72	10	139	15	12.1	1.33	5
79	9	162	16	11.0	195	9	124	13	11.7	1.23	3
207	8	146	19	15.0	320	8	111	12	12.1	1.58	7
254	7	127	22	21.0	396	7	99	15	17.9	1.47	7
269	6	105	26	32.9	430	6	84	20	31.2	1.30	6
322	5	79	30	61.2	488	5	64	22	52.4	1.36	8
346	4	49	26	113.0	519	4	42	21	100.0	1.24	5
395	3	23	16	228.6	586	3	21	14	200.0	1.14	2
395	2	7	5.8	483.3	586	2	7	5.9	536.4	0.98	-0.1
395	1	1.2	1.2	..	586	1	1.1	1.1	..	1.09	0.1

The superior growth of male rock bass is much more striking with respect to weight than length, although advantages of the males in terms of the number of years required to attain certain weights are of necessity the same as the advantages in the number of years required to reach the corresponding lengths (p. 234).

The years of life in which the males enjoyed the greatest actual and the greatest relative advantage in growth in weight were not the same. The greatest absolute advantage of 8 grams occurred in the fifth year but the greatest relative advantage was in the eighth (weight increment of males 1.58 times that of females). It will be noticed that these maximum advantages of the males with respect to growth in weight occurred one year later than the corresponding greatest advantages with respect to growth in length (fourth and seventh years of life—p. 234). It is true also that the relative advantages of the males were larger for growth in weight than for growth in length (larger ratios of increments in Table 20 than in Table 19). This greater relative advantage of the males in growth in weight accounts

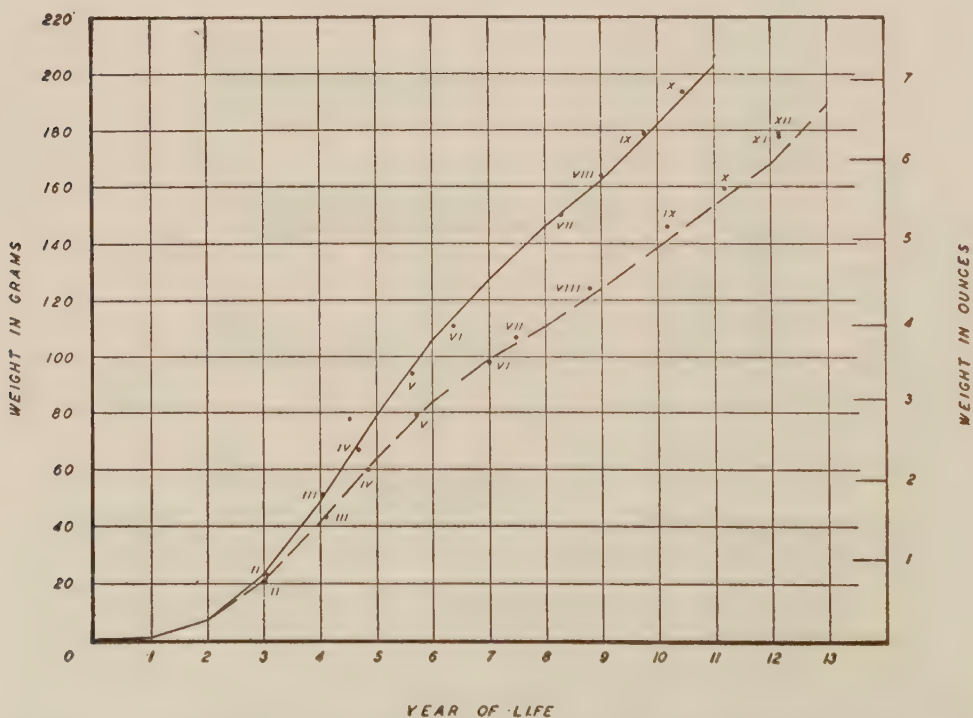


FIGURE 10. Calculated weight of the Nebish Lake rock bass at the end of each year of life. Solid line males, broken line females. The dots show the grand average weights the age-groups at capture.

for the pronounced divergence of the curves for the sexes in Figure 10.

The annual increments of growth in weight (ΔW) of both sexes increased continuously from the first year of life to a maximum in the fifth. The weight increments of the males decreased during the next four years of life but were large in the tenth and eleventh years. The changes in the increments of growth in weight of females beyond the fifth year were irregular. With the exception of the 21-gram growth in the thirteenth year (one fish) the annual weight increments of the females for all years of life later than the sixth fell within the range, 12 to 15 grams.

The percentage growth rate in weight in the second year of life was roughly 500 per cent for both sexes. The growth rate decreased rapidly in later years and did not exceed 20 per cent beyond the sixth year of life of the females or beyond the seventh year of life of the males.

COMPARISON OF THE GROWTH OF THE NEBISH LAKE ROCK BASS WITH THE GROWTH OF THE ROCK BASS IN OTHER LOCALITIES

Growth data based on the examination of scales of rock bass have been published by Wright (1929) for Trout and Muskellunge Lakes in northern Wisconsin and by Hile (1931) for Wawasee and Syracuse Lakes in northern Indiana. Trout Lake lies about 4 kilometers west of Nebish Lake and Muskellunge about 3 kilometers to the southwest.

Neither Wright nor Hile made a division of data according to sex. Hile made no growth calculations from scale measurements. Wright did present growth calculations from scale measurements, but based his calculations on the assumption that the ratio of body length to scale length (radius) is constant beyond the time of formation of the first annulus. Wright's data included no information as to growth in weight.

Because of the defects in the data presented by Wright and Hile, the most valid comparisons of the growth of rock bass in different localities appear to be those based on the average lengths (and weights, when available) of the age groups at capture, with the data for the sexes combined. This type of tabulation of available data on the growth of the rock bass appears in Table 21. The averages for the Trout Lake and Muskellunge

Lake rock bass are the weighted means of the averages given by Wright for his 1927 and 1928 collections separately. The combination of the 1927 and 1928 data from Trout Lake has been made in spite of Wright's expressed belief that the two collections, which were taken at different localities, represent distinct races within the lake. His belief was based on differences in the growth rate of the rock bass in the two collections. However, Wright had no sex records for his specimens; neither was he in position to determine the effect of gear selection on his samples. The relatively rapid growth of the Trout Lake rock bass taken in 1927 as compared to the fish captured in 1928 well may have resulted in a large measure from a great abundance of the more rapidly growing males in the sample and/or on the selective action of the fishing gear. The averages for the Lake Wawasee rock bass are based on the combination of scattered collections made over the 4-year period, 1926 to 1929. The 13 rock bass from Syracuse Lake all were taken during the summer of 1927.

TABLE 21. *Standard lengths (in millimeters) and weights (in grams) of the age groups of rock bass in collections from three northern Wisconsin and two northern Indiana lakes. The data for the sexes are combined. Numbers of individuals are in parentheses.*

Age group	Nebish		Trout	Muskellunge	Wawasee		Syracuse	
	Length	Weight	Length	Length	Length	Weight	Length	Weight
VII	161 (123)	123 (123)	146 (27)	139 (57)	230 (4)	349 (4)	..	..
VI	152 (49)	108 (49)	131 (42)	125 (74)	227 (1)	365 (1)	..	..
V	143 (111)	96 (111)	114 (39)	103 (63)	192 (5)	255 (5)	..	..
IV	130 (55)	67 (55)	..	..	182 (8)	199 (8)	..	..
III	117 (116)	46 (116)	..	..	147 (10)	107 (10)	129 (1)	72 (1)
II	92 (156)	22 (156)	..	..	111 (8)	46 (8)	100 (8)	33 (8)
I	..	..	..	..	55 (20)	5 (14)	59 (4)	6 (4)

The growth of rock bass from northern Indiana is far superior to that of northern Wisconsin rock bass. As an illustration, the III-group rock bass from Lake Wawasee were longer than the V-group fish from Nebish Lake and the VII-group rock bass from Trout and Muskellunge Lakes. Comparisons of Table 21 with the data of Tables 9 and 10 reveal that the size of Wawasee rock bass of age-group V approximated the maximum at-

tained by Nebish Lake fish regardless of age, and that Wawasee rock bass older than age-group V were much larger than the largest fish taken from Nebish Lake. The growth of the rock bass from Syracuse Lake appears to resemble that of the Lake Wawasee population. Age-group I from Syracuse Lake averaged larger and age-group II smaller than Lake Wawasee fish of corresponding age. Only one fish of age-group III was captured in Syracuse Lake.

That relatively good growth may be characteristic of the rock bass in the lakes of northern Indiana is suggested by Evermann and Clark's (1920) observation that in Lake Maxinkuckee the, ". . . . Rock Bass . . . reaches a length of about 12 or 13 inches and a weight of a little less than one pound. The great majority of those caught weigh a half pound or less." In Nebish Lake very few rock bass attain a weight of a half pound.

We can only speculate as to the causes for the superior growth of the rock bass from northern Indiana. Possible contributing factors are higher water temperatures (and in consequence, a probably longer growing season), more abundant food, lesser population densities, and a hereditarily greater capacity for growth.

A comparison of the growth of rock bass in the three northern Wisconsin lakes reveals that the growth of the Nebish Lake stock is superior to that of rock bass in the two neighboring lakes, Trout and Muskellunge. In the age groups for which comparisons are available the advantage of the Nebish Lake fish amounts to roughly two years of growth.

The rock bass is the third species from the lakes of northeastern Wisconsin in which the best growth has been found to occur in a lake with a relatively low productive capacity as estimated from the concentration of bound CO_2 in its waters. A summary of the relationship between the growth rates of the yellow perch, the cisco, and the rock bass in certain northeastern Wisconsin lakes and the average concentration of bound CO_2 in the surface waters is given in Table 22. The growth of the yellow perch was studied by Schneberger (1935) and that of the cisco by Hile (1936a).

In general, the growth rates (in length) of the different stocks of the three species tend to vary inversely with the esti-

TABLE 22. *Relationship between the rate of growth (in length) of three species of fish and the concentration of bound CO₂ (average surface conditions) in parts per million in certain lakes of the northeastern highlands, Wisconsin. In the order of growth rate the stock with the slowest growth has been assigned the value 1.*

Lake	Concentration of bound CO ₂ in p.p.m.	Rate of growth		
		Perch	¹ Cisco	Rock bass
Weber	¹ 1.2	2	..	..
Clear	² 2.2	..	4	..
Nebish	4.0	3	..	3
Muskellunge	10.0	..	3-2	1
Silver	15.0	1	2-3	..
Trout	18.5	..	1	2

¹ These values apply to the lakes at the time of the collection of material for the study of the rate of growth. Since the addition of lime in 1933 and 1934 the concentration of bound CO₂ in Weber Lake has stood at 2.0 p.p.m. Since 1935 the average value for Clear Lake has been 2.5 p.p.m.

² The positions of the Muskellunge Lake cisco and the Silver Lake cisco, respectively, were 2 and 3 with respect to growth in weight and 3 and 2 with respect to growth in length.

mated productive capacities of the lakes they inhabit. In the cisco the inverse relationship holds without exception. The order of the four lakes with respect to the rate of growth in length of their cisco populations (from the most rapidly to the most slowly growing) is precisely the reverse of their order with respect to the concentration of bound CO₂ in the surface waters. The relationship is not so clear-cut for the perch and rock bass. The best growth of perch does not occur in the lake with the lowest concentration of bound CO₂, but the poorest growth is to be found in the lake that is richest in bound CO₂ (Silver Lake). With reference to the rock bass, the lake with the lowest concentration of bound CO₂ (Nebish Lake) does contain the most rapidly growing population but the poorest growth does not occur in the lake with the highest estimated productive capacity (Trout Lake). However, neither the perch nor the rock bass enjoyed its best growth in the lake with highest estimated productive capacity or its poorest growth in the lake with the lowest estimated productive capacity. It is significant that the three species that show a correlation of good growth with a low concentration of bound CO₂ represent three different families—Percidae, Coregonidae, and Centrarchidae.

Schneberger and Hile were able to demonstrate also a correlation between the growth rates and population densities of the

perch and cisco, respectively. The general relationship was such that lakes with high concentrations of bound CO_2 had dense populations with a poor rate of growth, whereas the population was sparse and the growth rate good in lakes with low concentrations of bound CO_2 . Schneberger made no definite statement as to the probable manner in which the population density may affect the growth rate of perch. Hile suggested that the correlation between population density and the rate of growth in the cisco "... may depend on differences in the severity of the competition for food, or upon the operation of a 'space-factor', whereby crowding impedes growth independently of the abundance of food."

There are at present no data available for the detection of a possible correlation between the growth rates and population densities of rock bass in the three northern Wisconsin lakes. In a later section of this paper (p. 275), however, evidence will be presented for a possible correlation between annual fluctuations in the growth rate and the population density of the Nebish Lake rock bass stock.

FLUCTUATIONS IN THE ABUNDANCE OF YEAR CLASSES AND IN GROWTH RATE

ABUNDANCE OF AGE GROUPS AND YEAR CLASSES

A tabulation of the age and year-class composition of each year's collection of the Nebish Lake rock bass appears in Table 23. At the bottom of the table may be seen the numerical and percentage representations of the different year classes for all collections combined. In order to keep the large 1931 and 1932 collections comparable, the samples taken by hook and line, which method tended to capture only the larger and older fish, were excluded from the compilations of data for those years. The specimens taken by hook and line were retained, however, in the compilation of the 1930 data since it was believed that their inclusion would compensate the small amount of fishing with large-mesh gill nets (p. 194) and thus make the 1930 data more nearly comparable with those of later years. No rock bass were taken by hook and line in 1935. Since the percentage occurrence of the age groups and year classes of the males and

TABLE 23. Numerical and percentage representation of the year classes of the Nebish Lake rock bass in the different years' collections and in all collections combined.

Year of Capture	Item	Year class												Total	
		1919	1920	1921	1922	1923	1924	1925	1926	1927	1928	1929	1930		1931
1930	Age group	..	X	IX	VIII	VII	VI	V	IV	III	II	..	..	..	..
	Number of males	..	..	2	3	15	3	9	9	..	..	..	..	..	..
	Number of females	..	..	2	43	58	6	6	9	..	..	..	..	..	..
	Number, sexes combined	..	..	4	11	72	9	15	24	9	9	21	..	..	..
	Percentage	..	0.7	2.6	7.2	38.2	5.9	9.9	15.8	5.9	13.8	..	..	..	..
1931	Age group	XII	XI	X	IX	VIII	VII	VI	V	IV	III	II	..	..	..
	Number of males	..	..	4	18	115	27	5	8	3	6	10	..	..	..
	Number of females	1	..	17	47	99	24	11	7	5	7	9	..	..	..
	Number, sexes combined	1	2	21	65	214	51	16	15	8	14	60	..	..	..
	Percentage	0.2	0.4	4.5	13.9	45.8	10.9	3.5	3.2	1.7	3.0	12.9	..	..	..
1932	Age group	XIII	XII	XI	X	IX	VIII	VII	VI	V	IV	III	II	..	..
	Number of males	..	..	3	10	40	7	3	3	8	7	41	78	..	..
	Number of females	1	..	13	33	68	9	6	6	2	9	59	268	..	..
	Number, sexes combined	1	3	16	43	108	16	9	9	10	16	100	137	..	..
	Percentage	0.2	0.7	3.4	9.2	23.1	3.4	1.9	1.9	2.1	3.4	21.4	29.3	..	..
1935	Age group	..	..	..	..	..	XI	X	..	VIII	..	VI	V	IV	III
	Number of males	..	..	..	..	..	..	1	..	..	..	4	28	5	..
	Number of females	..	..	..	..	..	..	1	..	..	..	5	43	8	..
	Number, sexes combined	..	..	..	..	..	..	1	..	..	..	13	71	13	..
	Percentage	..	..	..	..	..	1.0	1.0	..	1.0	..	12.9	70.2	12.9	1.0
All collections	Males, all age groups	..	..	9	31	170	37	18	20	11	13	55	106	5	475
	Females, all age groups	2	6	32	88	210	40	23	22	8	16	77	102	8	635
	Sexes combined, all age groups	2	6	41	119	380	77	41	48	28	51	173	208	13	1,188
	Percentage	0.2	0.5	3.4	10.0	32.0	6.5	3.4	4.0	4.0	2.4	4.3	14.6	17.5	1.1

females were similar the data for the sexes were combined for the computation of the percentages.

In all years' collections the representations of the different age groups were decidedly unequal. In 1930, 58 or 38.2 per cent of the total collection of 152 rock bass were in the eighth year of life (age-group VII). No other age group, older or younger, contained even half as many fish. Still more striking was the dominance of the 1931 VIII-group which made up 45.8 per cent of the entire collection and contained more than three times as many fish as the next strongest age group (age-group IX). There was a less pronounced dominance in 1932. The dominant II-group (29.3 per cent of the total) was only slightly stronger than age-groups IX and III (23.1 and 21.4 per cent respectively, of the total collection). The 1935 collection contains the outstanding example of overwhelming dominance of a single age group. In this year 70.2 per cent of the rock bass were in the sixth year of life (age-group V).

On the whole, 1930-1932 collections were characterized by an abundance of old fish (age-group VII and older) and a scarcity of fish of medium age (age-group IV to age-group VI). Age-group II was fairly well represented (12.9 to 29.3 per cent) in all years but only the 1932 material contained a large number of III-group rock bass. Exceptions to the above general statement are offered by the weak VII- and VIII-groups of 1932 and the relatively strong 1930 IV-group. The distribution of ages in 1935 was precisely the reverse of conditions in 1930 to 1932. In 1935, 96.0 per cent of the rock bass belonged to age-groups IV, V, and VI.

The examination of the percentage distributions of the age groups in relation to their year of origin suggests that the unequal representations of the different age groups may be in large measure due to the varying degrees of success of natural reproduction in different calendar years. For example, the 1923 year class which was dominant in 1930 (age-group VII) and 1931 (age-group VIII) and was still strong as the 1932 IX-group must have been very abundant. The 1930 year class also appears to have been strong in numbers. This year class provided the dominant II-group of 1932 and accounted for 70.2 per cent of the 1935 collection. The 1927 year class on the other hand must

have been relatively weak since it was poorly represented in all years' collections.

Although the data of Table 23 point rather conclusively to the presence of relatively rich and poor year classes in the Nebish Lake rock bass population, they do not provide an exact measure of the true relative strength of the year classes. The most important difficulties in the interpretation of the material are related to the disturbing effect of the age at which the year classes appeared in the collections and to gear selectivity. As an illustration of the significance of age it may be pointed out that the 16 XI-group rock bass of the 1932 collection indicate a far greater original abundance for the 1921 year class than the 16 IV-group fish indicate for the 1928 year class. The two year classes were represented by equal numbers of fish in the collection, but at the time of sampling the 1921 year class had been subjected to 7 more years of natural mortality, not to mention the greater exposure to fishing. Consequently the 1921 year class safely can be held to have been originally much the stronger. The percentage representation of the two year classes in all collections combined (1921—3.4 per cent; 1928—4.3 per cent) gives no cause to doubt the above conclusion. Assuming that the samples are adequate, it is true generally that a strong representation of an old age group indicates a much richer year class than does an equally large number of fish several years younger. On the other hand, a scarcity of old fish may be merely the result of natural mortality over a long period of years, whereas a scarcity of fish in a young age group is definitely suggestive of a poor year class.

The effect of gear selection also has an important bearing on the interpretation of the data of Table 23. It has been stated already (p. 197) that the smaller II-group fish are not taken readily by gill nets. As a result the II-group samples all probably contained too few fish. Furthermore, the failure of the gear to take any I-group and 0-group fish caused certain year classes to be totally absent in some years' collections. The 1929 and 1930 year classes were not represented in the 1930 material, and the members of the latter year class were lacking also in 1931. The 1931 and 1932 year classes either were not yet hatched or were too small to be captured at the time of all but the 1935 col-

lections. The effect of gear selection was doubtless much less severe among the older fish, although there is reason to believe that the addition of a mesh size larger than those employed would have led to the capture of more old fish, especially in 1932 (p. 197).

Despite the obvious defects in the data the differences in the representation of the several year classes are so great that a number of them can be classified reasonably safely by such terms as strong, weak, or of moderate strength. The following estimate of the relative abundance of the year classes was based on the careful examination of their representation in the different years' collections with allowance made for age at capture and the probable effect of gear selection. The year classes have been arranged in their estimated order of abundance from the strongest to the weakest.

Exceptionally strong year classes

1923 year class—was dominant as the 1930 VII-group (38.2 per cent) and as the 1931 VIII-group (45.8 per cent) and was very strong as the IX-group of 1932 (23.1 per cent). The great abundance of the year class at such high ages marks it as one of unusual strength.

1930 year class—was dominant in the 1932 collection (29.3 per cent) and made up 70.2 per cent of the 1935 collection. Although there are no gear records for the 1935 material, the statement by the collectors that nets of several sizes of mesh were fished (p. 194) and the excessive abundance of the V-group leave little doubt as to the great strength of the 1930 year class.

Moderately strong to normal year classes

1922 year class—in spite of its advanced age at capture (VIII to X), had a representation of 7.2 to 13.9 per cent in the 1930-1932 collections and made up 10.0 per cent of all collections combined.

1921 year class—was not very strongly represented (2.6 to 4.5 per cent) in the 1930-1932 collections but even this small representation at ages from IX to XI marks the year class as fairly strong. The 1921 year class was probably consider-

ably weaker than the 1922 year class.

Normal to moderately weak year classes

1929 year class—contributed the strongest III-group (21.4 per cent in 1932) but was not exceptionally abundant as the 1931 II-group (12.9 per cent) and the 1935 VI-group (12.9 per cent).

1924 year class—had a fair representation as the 1931 VII-group (10.9 per cent) but was relatively weak as the 1930 VI-group and as the 1932 VIII-group (5.9 and 3.4 per cent, respectively).

Exceptionally weak year classes

1926 year class—was moderately abundant as the 1930 IV-group (15.8 per cent), but this good representation was counter-balanced by the low percentages in 1931 and 1932 (3.2 and 1.9 per cent, respectively).

1925 year class—was fairly strong as the 1930 V-group (9.9 per cent) but was weak in 1931 and 1932 (3.5 and 1.9 per cent, respectively).

1928 year class—as the age-group II made up 13.8 per cent of the 1930 collection but was weak in 1931 and 1932 (3.0 and 3.4 per cent, respectively).

1927 year class—was poorly represented in all collections (from 1.7 to 5.9 per cent over the period, 1930 to 1932) and accounted for only 2.4 per cent of all collections combined.

Year classes of uncertain strength

1919 and 1920 year classes—were represented by such old fish (X to XIII) that it is impossible to judge accurately whether their scarcity is to be attributed to great age or to originally weak year classes.

1931 and 1932 year classes—could not be evaluated satisfactorily since their occurrence was limited to the 1935 collection for which gear records are lacking.

The order of arrangement of the year classes in the preceding outline is to a certain extent a matter of personal judgment, and

may not conform exactly to the true conditions. Decisions concerning the ranking of certain year classes were extremely difficult to make. Nevertheless, the following general summary may be considered valid. Relatively abundant year classes were produced over the period 1921 to 1923; the 1923 year class was phenomenally successful. The 1924 year class was much less abundant than the 1923 year class but was stronger than the exceptionally weak year classes of 1925 to 1928. The 1929 year class was more abundant than those of the four preceding years, and the 1930 year class was again one of exceptional strength. The fluctuations in abundance of the year classes offer a suggestion of a cycle with maxima in 1923 and 1930.

ANNUAL DIFFERENCES IN GROWTH RATE

Materials for the study of annual fluctuations in the growth rate of the Nebish Lake rock bass may be found in Tables 24 and 25. The arrangement of the tables is such that the vertical columns show the (calculated) growth made by fish in different years of life but in the same calendar year, and the horizontal rows offer a comparison of the growth in different calendar years for the same year of life. Each diagonal row gives the growth history of a single year class. For example, the males of the 1921 year class grew 38 millimeters in the first year of life (1921), 32 millimeters in the second (1922), 31 millimeters in the third (1923)

The plus and minus signs which have been introduced to facilitate the examination of the data indicate whether a particular growth increment is greater or less than the corresponding growth increment for the preceding calendar year. As an illustration, the 31-millimeter growth made by males in the second year of life in 1923 was less than the 32-millimeter growth made by fish of the same age in 1922. Consequently the 31 has been followed by a minus sign. Similarly the 26-millimeter increment of the second-year fish in 1924 represents a further decrease. The growth of the second-year rock bass improved, however, in 1925, and the 30 was followed by a plus sign. Where there was no change the sign was omitted.

The annual fluctuations in the growth of the first year of life are so obviously independent of those of later years that in the

TABLE 25. Annual increments of growth in length (in millimeters) of the females of the various year classes of the Nebish Lake rock bass.

Year of life	Increment of growth in calendar years											Unweighted mean
	1920	1921	1922	1923	1924	1925	1926	1927	1928	1929	1930	
12	..	..	..	..	..	..	..	..	..	..	..	7
11	..	..	..	..	..	..	..	..	..	..	..	6
10	..	..	..	..	..	..	..	..	..	..	..	5
9	..	..	..	..	..	..	..	..	..	..	..	6
8	..	..	..	..	..	..	..	..	..	..	..	6
7	..	..	..	..	..	..	..	..	..	..	..	6
6	..	..	..	..	..	..	..	..	..	..	..	8
5	..	..	..	..	..	..	..	..	..	..	..	13
4	..	..	..	..	..	..	..	..	..	..	..	18
3	..	..	..	..	..	..	..	..	..	..	..	24
2	..	..	..	..	..	..	..	..	..	..	..	27
1	..	..	..	..	..	..	..	..	..	..	..	27
1	32	36 +	36	36	36	35 -	30 -	30	30	29 -	30 +	32
2	36 +	36 +	36	36	36	35 -	30 -	30	30	29 -	30 +	28 -
3	28	28	32 +	30 -	28 -	28	27 -	24 -	20 -	25 +	26 +	30 -
4	28	28	31	28	22 -	21 -	18 +	17 -	17	19 +	21 +	21
5	..	..	..	..	..	..	..	..	11	12 +	14 +	20 +
6	..	..	..	..	..	..	..	..	8	6	7 +	12 +
7	..	..	..	..	..	..	..	..	6	5 -	5	7
8	..	..	..	..	..	..	..	..	7	4	4	8 +
9	..	..	..	..	..	..	..	..	..	..	..	7 +
10	..	..	..	..	..	..	..	..	..	..	..	8 +
11	..	..	..	..	..	..	..	..	..	..	..	7
12	..	..	..	..	..	..	..	..	..	..	..	8 +
13	..	..	..	..	..	..	..	..	..	..	..	7
14	..	..	..	..	..	..	..	..	..	..	..	8 +
15	..	..	..	..	..	..	..	..	..	..	..	7
16	..	..	..	..	..	..	..	..	..	..	..	8 +
17	..	..	..	..	..	..	..	..	..	..	..	7
18	..	..	..	..	..	..	..	..	..	..	..	8 +
19	..	..	..	..	..	..	..	..	..	..	..	7
20	..	..	..	..	..	..	..	..	..	..	..	8 +
21	..	..	..	..	..	..	..	..	..	..	..	7
22	..	..	..	..	..	..	..	..	..	..	..	8 +
23	..	..	..	..	..	..	..	..	..	..	..	7
24	..	..	..	..	..	..	..	..	..	..	..	8 +
25	..	..	..	..	..	..	..	..	..	..	..	7
26	..	..	..	..	..	..	..	..	..	..	..	8 +
27	..	..	..	..	..	..	..	..	..	..	..	7
28	..	..	..	..	..	..	..	..	..	..	..	8 +
29	..	..	..	..	..	..	..	..	..	..	..	7
30	..	..	..	..	..	..	..	..	..	..	..	8 +
31	..	..	..	..	..	..	..	..	..	..	..	7
32	..	..	..	..	..	..	..	..	..	..	..	8 +
33	..	..	..	..	..	..	..	..	..	..	..	7
34	..	..	..	..	..	..	..	..	..	..	..	8 +
35	..	..	..	..	..	..	..	..	..	..	..	7
36	..	..	..	..	..	..	..	..	..	..	..	8 +
37	..	..	..	..	..	..	..	..	..	..	..	7
38	..	..	..	..	..	..	..	..	..	..	..	8 +
39	..	..	..	..	..	..	..	..	..	..	..	7
40	..	..	..	..	..	..	..	..	..	..	..	8 +
41	..	..	..	..	..	..	..	..	..	..	..	7
42	..	..	..	..	..	..	..	..	..	..	..	8 +
43	..	..	..	..	..	..	..	..	..	..	..	7
44	..	..	..	..	..	..	..	..	..	..	..	8 +
45	..	..	..	..	..	..	..	..	..	..	..	7
46	..	..	..	..	..	..	..	..	..	..	..	8 +
47	..	..	..	..	..	..	..	..	..	..	..	7
48	..	..	..	..	..	..	..	..	..	..	..	8 +
49	..	..	..	..	..	..	..	..	..	..	..	7
50	..	..	..	..	..	..	..	..	..	..	..	8 +
51	..	..	..	..	..	..	..	..	..	..	..	7
52	..	..	..	..	..	..	..	..	..	..	..	8 +
53	..	..	..	..	..	..	..	..	..	..	..	7
54	..	..	..	..	..	..	..	..	..	..	..	8 +
55	..	..	..	..	..	..	..	..	..	..	..	7
56	..	..	..	..	..	..	..	..	..	..	..	8 +
57	..	..	..	..	..	..	..	..	..	..	..	7
58	..	..	..	..	..	..	..	..	..	..	..	8 +
59	..	..	..	..	..	..	..	..	..	..	..	7
60	..	..	..	..	..	..	..	..	..	..	..	8 +
61	..	..	..	..	..	..	..	..	..	..	..	7
62	..	..	..	..	..	..	..	..	..	..	..	8 +
63	..	..	..	..	..	..	..	..	..	..	..	7
64	..	..	..	..	..	..	..	..	..	..	..	8 +
65	..	..	..	..	..	..	..	..	..	..	..	7
66	..	..	..	..	..	..	..	..	..	..	..	8 +
67	..	..	..	..	..	..	..	..	..	..	..	7
68	..	..	..	..	..	..	..	..	..	..	..	8 +
69	..	..	..	..	..	..	..	..	..	..	..	7
70	..	..	..	..	..	..	..	..	..	..	..	8 +
71	..	..	..	..	..	..	..	..	..	..	..	7
72	..	..	..	..	..	..	..	..	..	..	..	8 +
73	..	..	..	..	..	..	..	..	..	..	..	7
74	..	..	..	..	..	..	..	..	..	..	..	8 +
75	..	..	..	..	..	..	..	..	..	..	..	7
76	..	..	..	..	..	..	..	..	..	..	..	8 +
77	..	..	..	..	..	..	..	..	..	..	..	7
78	..	..	..	..	..	..	..	..	..	..	..	8 +
79	..	..	..	..	..	..	..	..	..	..	..	7
80	..	..	..	..	..	..	..	..	..	..	..	8 +
81	..	..	..	..	..	..	..	..	..	..	..	7
82	..	..	..	..	..	..	..	..	..	..	..	8 +
83	..	..	..	..	..	..	..	..	..	..	..	7
84	..	..	..	..	..	..	..	..	..	..	..	8 +
85	..	..	..	..	..	..	..	..	..	..	..	7
86	..	..	..	..	..	..	..	..	..	..	..	8 +
87	..	..	..	..	..	..	..	..	..	..	..	7
88	..	..	..	..	..	..	..	..	..	..	..	8 +
89	..	..	..	..	..	..	..	..	..	..	..	7
90	..	..	..	..	..	..	..	..	..	..	..	8 +
91	..	..	..	..	..	..	..	..	..	..	..	7
92	..	..	..	..	..	..	..	..	..	..	..	8 +
93	..	..	..	..	..	..	..	..	..	..	..	7
94	..	..	..	..	..	..	..	..	..	..	..	8 +
95	..	..	..	..	..	..	..	..	..	..	..	7
96	..	..	..	..	..	..	..	..	..	..	..	8 +
97	..	..	..	..	..	..	..	..	..	..	..	7
98	..	..	..	..	..	..	..	..	..	..	..	8 +
99	..	..	..	..	..	..	..	..	..	..	..	7
100	..	..	..	..	..	..	..	..	..	..	..	8 +
101	..	..	..	..	..	..	..	..	..	..	..	7
102	..	..	..	..	..	..	..	..	..	..	..	8 +
103	..	..	..	..	..	..	..	..	..	..	..	7
104	..	..	..	..	..	..	..	..	..	..	..	8 +
105	..	..	..	..	..	..	..	..	..	..	..	7
106	..	..	..	..	..	..	..	..	..	..	..	8 +
107	..	..	..	..	..	..	..	..	..	..	..	7
108	..	..	..	..	..	..	..	..	..	..	..	8 +
109	..	..	..	..	..	..	..	..	..	..	..	7
110	..	..	..	..	..	..	..	..	..	..	..	8 +
111	..	..	..	..	..	..	..	..	..	..	..	7
112	..	..	..	..	..	..	..	..	..	..	..	8 +
113	..	..	..	..	..	..	..	..	..	..	..	7
114	..	..	..	..	..	..	..	..	..	..	..	8 +
115	..	..	..	..	..	..	..	..	..	..	..	7
116	..	..	..	..	..	..	..	..	..	..	..	8 +
117	..	..	..	..	..	..	..	..	..	..	..	7
118	..	..	..	..	..	..	..	..	..	..	..	8 +
119	..	..	..	..	..	..	..	..	..	..	..	7
120	..	..	..	..	..	..	..	..	..	..	..	8 +
121	..	..	..	..	..	..	..	..	..	..	..	7
122	..	..	..	..	..	..	..	..	..	..	..	8 +
123	..	..	..	..	..	..	..	..	..	..	..	7
124	..	..	..	..	..	..	..	..	..	..	..	8 +
125	..	..	..	..	..	..	..	..	..	..	..	7
126	..	..	..	..	..	..	..	..	..	..	..	8 +
127	..	..	..	..	..	..	..	..	..	..	..	7
128	..	..	..	..	..	..	..	..	..	..	..	8 +
129	..	..	..	..	..	..	..	..	..	..	..	7
130	..	..	..	..	..	..	..	..	..	..	..	8 +
131	..	..	..	..	..	..	..	..	..	..	..	7
132	..	..	..	..	..	..	..	..	..	..	..	8 +
133	..	..	..	..	..	..	..	..	..	..	..	7
134	..	..										

discussions of changes in growth rate the first-year growth and that of the second and later years of life have been treated separately. The growth beyond the first year will be considered first.

Growth in the Second and Later Years of Life

The increments of Tables 24 and 25 demonstrate that the amount of growth made by fish in a particular year of life is subject to a wide variation from year to year. The second-year growth of the males varied from 22 millimeters in 1927 and 1928 to 32 in 1922; that of the females ranged from 21 millimeters in 1928 to 32 in 1922 and 1923. Similar fluctuations occurred in the growth increments of both sexes in later years of life.

It may be seen also that in some calendar years the growth increments tended to increase or decrease consistently in comparison with corresponding increments of the preceding year and, further, that in certain years the amount of growth made by rock bass at all ages (exclusive of the first year) tended consistently to be relatively high or low. Six comparisons are possible between the growth of male rock bass in 1927 and 1928 (Table 24). In four years of life (third, fourth, sixth, and seventh) the 1928 growth was below that of 1927. The remaining two comparisons (second and fifth years) showed no differences. Furthermore, the 1928 growth increments were generally lower than those for fish of the same age in other calendar years. The 1929 growth, on the other hand, showed improvement in five of the seven comparisons with 1928. Growth in 1929 can not be described, however, as outstandingly good. The most consistently large growth increments occurred in 1931. The data for some years contain certain inconsistencies. The comparison of the growth increments of 1924 and 1925, for example, shows one decrease (fourth year) and two increases (second and third years) in 1925. Similarly, two of the 1926 growth increments were greater than those of 1925, one increment was less, and one was the same.

The fluctuations in the growth of the females (Table 25) bear a general resemblance to those of the males. As was true for the males, the growth of the females in 1928 was generally poor, although the decrease in comparison with 1927 was not as

great as for the males; improvement in growth was general in 1929; the 1931 growth increments were exceptionally large; and the data for certain years (as 1925 and 1926) did not give consistent indication of improvement or decline in growth.

Certain generalizations concerning growth in the second and later years of life can be drawn safely from the data of Tables 24 and 25. The growth of both males and females was fairly good in 1922 and 1923. The year 1924 saw the beginning of an irregular but definite downward trend in growth that culminated in the very poor growth of 1927 and 1928. A sharp upturn in growth rate occurred in 1929. This improvement continued through 1931 in which year the growth was exceptionally good.

The description in the preceding paragraph, although valid, does not provide a very precise measure of annual fluctuations in the growth of the rock bass. Consequently, a detailed analysis was made of the growth data in order to determine more exactly the extent to which growth rate varied from year to year. The procedure consisted of the determination of the percentage change in the growth in each year in comparison with the growth of fish in corresponding years of life in the preceding year. Details of the method will be explained in the following paragraphs.

Table 24 shows that comparisons of the growth of males beyond the first year of life in 1922 and 1923 must be limited to the second-year increments of 32 millimeters and 31 millimeters respectively. These increments have been listed in Table 26 under the headings, "Growth in earlier year", and "Growth in later year". The mean of the increments is 31.5 millimeters, and the decrease of 1 millimeter in 1923 represents a change of -3.2 per cent from this mean.²³ The increments of growth for both

²³ The desirability of computing the percentage change in growth from the mean growth of the two years that are being compared rather than from the growth in the earlier of the two years may be seen from the following example. Let it be assumed that the growth increments of three consecutive years are 10, 8, and 10 millimeters. Growth in the second of the three years declined 20 per cent from growth in the first, and growth in the third year improved 25 per cent with respect to growth in the second. The successive addition of the percentages to determine the position of each year as to the quality of growth gives the following rankings for the three years: 0.0; -20.0 ; 5.0. Growth in the third year appears to have been better than that in the first. When the mean growth of the years that are being compared is employed for the computation of the percentage change in growth, the percentages for the three years are: 0.0; -22.2 ; 0.0.

the second and third years of life are available for the determination of the change in growth in 1924 as compared to 1923. In 1923 the combined second- and third-year growth increments of the male rock bass (31 and 31) gave a "total" growth of 62 millimeters. The 1924 growth was 26 millimeters for the second-year rock bass and 28 millimeters for the third-year fish. The "total" growth was 54 millimeters, a decrease of 8 millimeters. This difference was -13.8 per cent of the 1923-1924 mean "total" growth of 58 millimeters. The determination of the change in growth in each of the later years with respect to the growth of the year immediately preceding was made by a continuation of the above process. Each increase or decrease in "total" growth was expressed as a percentage of the mean total growth. The more recent the year under consideration the greater was the number of years of life involved in the determination.

TABLE 26. *Tabulation of data employed in the determination of annual fluctuations in the growth of male Nebish Lake rock bass. For explanation see text.*

Years involved in the comparison	Growth in earlier year	Growth in later year	Mean	Change in growth	Percentage change in growth
1922 and 1923	32	31	31.5	-1	-3.2
1923 and 1924	62	54	58.0	-8	-13.8
1924 and 1925	78	83	80.5	5	6.2
1925 and 1926	102	101	101.5	-1	-1.0
1926 and 1927	113	110	111.5	-3	-2.7
1927 and 1928	120	110	115.0	-10	-8.7
1928 and 1929	116	138	127.0	22	17.3
1929 and 1930	144	154	149.0	10	6.7
1930 and 1931	160	179	169.5	19	11.2

The percentage changes in growth in Table 26 were employed first to fix the position of each year with reference to "goodness of growth" in 1922. The 1923 growth was $0.0 - 3.2 = -3.2$ per cent below the 1922 level; the 1924 growth was $0.0 - 3.2 - 13.8 = -17.0$ per cent below that of 1922; the 1925 growth was $0.0 - 3.2 - 13.8 + 6.2 = -10.8$ per cent below the 1922 growth; . . . However, the 1922-1931 mean of the percentages determined in this manner was -7.4 , and the growth of the male rock bass in 1922 must have been 7.4 per cent above the 10-year average and not exactly average (0.0) as assumed originally. The deviation of each year's growth from the 1922 growth was

TABLE 27. Deviation of the growth of the Nebish Lake rock bass in different calendar years from the average for the 10-year period, 1922-1931. (First-year growth was excluded from the computations).

Sex	Percentage deviation from average growth in calendar year									
	1922	1923	1924	1925	1926	1927	1928	1929	1930	1931
Male	7.4	4.2	-9.6	-3.4	-4.4	-7.1	-15.8	1.5	8.2	19.4
Female	9.9	8.3	-8.6	-5.4	-5.4	-9.1	-14.7	-5.3	8.6	21.7
Average	8.6	6.2	-9.1	-4.4	-4.9	-8.1	-15.2	-1.9	8.4	20.6

converted, therefore, to a deviation from the 1922-1931 average growth by the addition of 7.4 per cent. These deviations from average growth are listed in Table 27. The procedure for the computation of the annual deviations of the growth of female rock bass from the average (listed in the same table) was identical with that just outlined for the males. The annual percentage deviations of the growth of both sexes from the 1922-1931 average are presented graphically in Figure 11.

The annual deviations of the growth of male and female rock bass from the 1922-1931 average agreed remarkably well. The close correspondence speaks well for the reliability of the original data and of the method employed, since the two sets of percentages were derived independently and from groups of fish with basically different rates of growth. (The males grow more rapidly than do the females.) The means of the percentage deviations of the sexes from the average growth (bottom of 27) may be used to describe the annual fluctuations in the growth of the Nebish Lake rock bass.

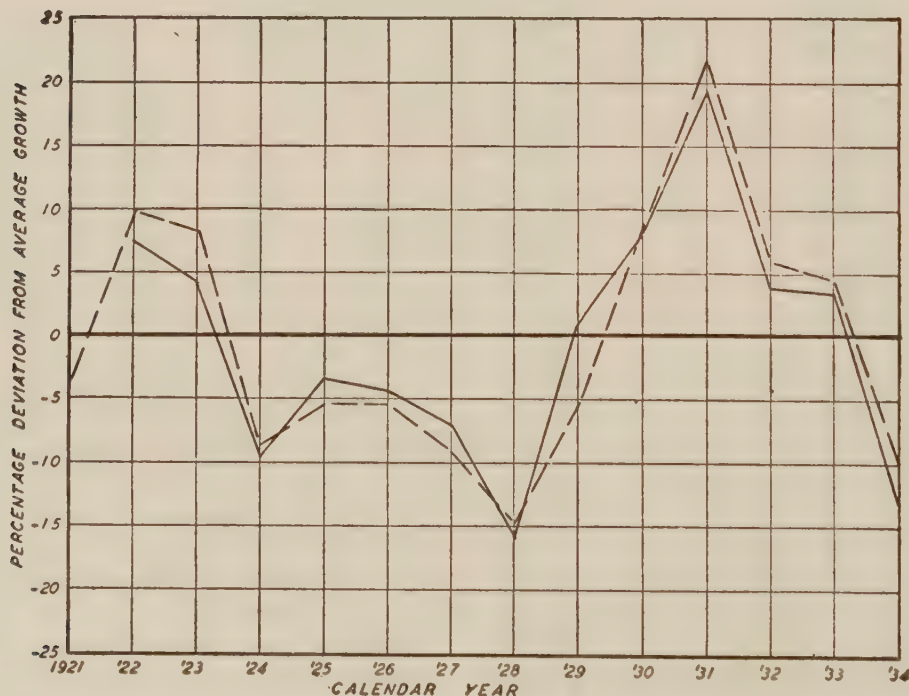


FIGURE 11. Annual percentage deviation of the growth of the Nebish Lake rock bass (in the second and later years of life) from the average for the period, 1922-1931. Solid line males, broken line females.

The growth of these rock bass stood at 8.6 per cent above average in 1922. A slight decline in 1923 was followed by a sharp drop to 9.1 per cent below average in 1924. Growth improved somewhat in 1925, although it was still below average, and remained at approximately the 1925 level in 1926. New declines in 1927 and 1928 reduced the growth to 15.2 per cent below average in the latter year. The next three years saw a rapid and consistent improvement which carried the growth to a point 20.6 per cent above average in 1931.

Possibly the most striking feature of the data on annual fluctuations in the growth of the Nebish Lake rock bass is the rapid improvement in growth from 15.2 per cent below average in 1928 to 20.6 per cent above average in 1931—a total change of 35.8 per cent of the average. Extensive changes in the growth rates of fish populations have been reported frequently, but these changes usually have been associated with disturbances within the population contingent upon the intensification or relaxation of fishing activities. The fluctuations in the growth of the Nebish Lake rock bass, on the contrary, may be considered representative of changes that occur under natural conditions, since there is no commercial fishery in the lake and the number of fish removed by anglers, prior to 1934 at least, was negligible. (The formerly rough and narrow road leading to Nebish Lake was improved in that year.)

Data that cover only a 10-year period are not adequate to demonstrate the presence or absence of cycles in the rate of growth. It should be mentioned, however, that 2 years of growth above average at the beginning of the period were followed by a period of 5 or 6 years of "subnormal" growth (the classification of 1929 must be held questionable), and that these poor-growth years were succeeded in turn by 2 or 3 years in which growth was again near or above average.

Only scattered data are available on annual fluctuations in growth outside the period, 1922 to 1931. An estimate of the growth in 1921 may be had from the second-year growth of females (Table 25). From the 1921 and 1922 increments of 28 and 32 millimeters respectively it may be computed that 1921 growth was 13.3 per cent below 1922 growth or 3.4 per cent below the 1922-1931 average.

The growth history of the abundant 1930 year class, as represented in the 1935 collection (age-group V) provides some information as to growth in the three years, 1932 to 1934. This same collection contained small representations of other year classes, but the lack of gear records in 1935 and the consequent lack of information concerning the probable selective action of the nets make it advisable to confine the analyses of the 1932-1934 growth to the data of the single well represented group.

The orientation of the growth of the 1930 year class in different calendar years with respect to the 1922-1931 average has been based on comparisons of the growth increments of the year class with the growth increments of fish in corresponding years of life over the period, 1925 to 1931. This period is the longest for which growth data are available for both sexes for all years of life involved (third, fourth, and fifth—see Tables 24 and 25). As an illustration of the procedure, in 1932 the males of the 1930 year class, then in their third year of life, grew 30.3 millimeters as compared with the 1925-1931 average of 29.1 millimeters for fish in their third year (Table 28). The deviation of the growth of the 1930 year class from the 1925-1931 growth was 4.0 per cent, but since the mean deviation of the 1925-1931 growth of male rock bass from the 1922-1931 average was -0.2 per cent (as determined from Table 27), the deviation of the 1930 year-class growth from the same 10-year average was $4.0 - 0.2$ or 3.8 per cent. Similarly the growth of the 1930 year-class males in their fourth year of life in 1933 had a deviation of 3.6 per cent from the average 1925-1931 growth for the same year of life and therefore of 3.4 per cent from the 1922-1931 average.

By the same procedure the 1932 growth of the females was found to deviate 7.3 per cent from the average 1925-1931 growth of female rock bass in their third year of life. The percentages of Table 27, however, showed that the 1925-1931 growth of female rock bass was 1.4 per cent below the 1922-1931 average. Therefore the percentage deviation of the growth of the 1930 year class in 1932 from the 1922-1931 average was $7.3 - 1.4 = 5.9$.

The agreement between the sexes with respect to the percentage departure from average growth over the period, 1932 to 1934, was only fair. The greatest discrepancy occurred in 1934

TABLE 28. *Growth increments (millimeters) of the 1930 year-class rock bass, in the years, 1932-1934, compared with average growth of fish in corresponding years of life, 1925-1931, together with estimates of the percentage deviation of the growth of 1930 year-class fish in different calendar years from the 1922-1931 average. The calendar years of the heading apply to the 1930 year class only.*

Item	Year of life and/or Calendar year		
	3	4	5
	1932	1933	1934
Growth of 1930 year-class males	30.3	28.4	19.3
Growth of males (1925-1931) in corresponding year of life	29.1	27.4	21.9
Deviation of 1930 year-class growth from 1922-1931 average	3.8	3.4	-12.8
Growth of 1930 year-class females	28.3	25.6	17.3
Growth of females (1925-1931) in corresponding year of life ..	26.3	24.1	18.3
Deviation of 1930 year-class growth from 1922-1931 average ..	5.9	4.6	-7.0
Deviation of 1930 year-class growth (average for sexes)	4.8	4.0	-9.9

in which year the percentages were -12.8 for the males and -7.0 for the females. The trends were the same, however, for both sexes. It appears valid, therefore, to conclude that the peak growth of 1931 was followed by a 3-year period of decline in growth rate.

Fluctuations in First-Year Growth

On p. 249 it was stated without explanatory discussion that the first-year growth of the Nebish Lake rock bass was "obviously independent" of growth in the second and later years of life. The examination of Tables 24 and 25 will reveal that the chief disagreement between the annual variations of first-year and later growth lay in the failure of the young of the year to share the general improvement in growth in the years, 1929 to 1931. It is true also that first-year growth was good in 1924 and 1925—years in which the growth of older fish was below average.

Details concerning annual variation in the first-year growth of Nebish Lake rock bass are presented in Table 29. The percentage deviations have been calculated with reference to the average first-year growth for the 10 years, 1922 to 1931.²⁴ The use of this period makes the percentages directly comparable with those for growth in the later years of life (Table 27).

²⁴ The averages were 32.8 millimeters for the males and 31.9 millimeters for the females.

TABLE 29. *Percentage deviations of first-year growth of the Nebish Lake rock bass in different calendar years from the 1922-1931 average*

Sex	Percentage deviation from average growth in calendar year											
	1920	1921	1922	1923	1924	1925	1926	1927	1928	1929	1930	1931
Male	..	15.9	18.9	12.8	22.0	0.6	-8.5	-11.6	-5.5	-11.6	-5.5	-11.6
Female	0.3	12.9	12.9	12.9	12.9	9.7	-6.0	-6.0	-6.0	-9.1	-9.1	-12.2
Average	0.3	14.4	15.9	12.8	17.4	5.2	-7.2	-8.8	-5.8	-10.4	-7.3	-11.9

Although the percentages for the sexes in Table 29 do not agree in detail, the general trends in the annual variation in first-year growth are similar. It appears to be justifiable to describe the yearly changes in first-year growth from the average percentages for the sexes. The growth of the first-summer rock bass was approximately at the 1922-1931 average in 1920. Growth improved in 1921 and 1922, fell back a little in 1923, and reached a maximum in 1924 (17.4 per cent above average). Two successive years of sharp decline reduced first-year growth from the 1924 peak to a point 7.2 per cent below average in 1926. Beyond this year the variations were irregular but growth was consistently below average. The poorest first-year growth of the 12-year period was made in 1931, the year in which older fish enjoyed their best growth. The comparison of the percentages of Table 29 with those of Table 27 substantiates fully the earlier contention that the annual fluctuations in first-year and later growth are independent.

At one time the possibility was considered that the disagreement between the annual fluctuations of first-year and later growth may have originated, in part at least, in some defect in the method of growth calculation. Since all collections were made in 1930 to 1932 and in 1935, it follows that in general, the more recent the calendar year for which growth was computed, the lower was the average age of the fish on which the calculations of first-year growth were based. Now if the method of growth calculation contained a defect whereby the older fish tended to have the larger calculated lengths at the ends of the first year, the consistently poor first-year growth in the more recent calendar years could be explained as apparent rather than real. To test this possibility a series of comparisons has been made between calculated lengths at the end of the first year

of life and the corresponding measurements of the anterior radius of the scale to the first annulus (Table 30).

TABLE 30. *Comparison of the average calculated lengths of rock bass of several age groups at the end of the first year of life with the body lengths corresponding to the average lengths of the anterior radii of key scales to the first annulus. The scales were measured at the magnification, X 40.5.*

Sex	Age group	Number of fish	Scale radius in millimeters to first annulus	Calculated length at end of first year of life	Length of fish corresponding to scale measurement
Male	IX	8	12.5	36	33.9
	III	15	10.3	28	29.6
	II	18	12.3	34	33.5
Female	IX	17	13.7	36	36.2
	IV	6	10.2	28	29.4
	III	13	10.0	28	29.0
	II	10	12.0	34	32.9

The data of Table 30 were based entirely on measurements of "key" scales²⁵ (see p. 209) and hence are free from the distortion that might result from selection of scales by size on the part of the technician who prepared the slides. It may be seen at once that the variations in l_1 are reflected in similar variations in the length of the anterior radius of the scale within the first annulus. The average calculated lengths are not in full agreement with the fish lengths corresponding to the actual scale measurements, but the discrepancies show no definite correlation with age. The length of fish (33.9 millimeters) corresponding to the average scale length (12.5 millimeters) was below the average calculated length (36 millimeters) in the IX-group males, but was equal to or possibly higher in the IX-group females (36.2 as compared to 36). Among the younger fish the average calculated lengths were too low in both III-groups and in the IV-group females, but were too high in both II-groups. The distribution of the discrepancies marks them as the result of random sampling rather than of errors introduced by the method of growth calculation and correlated with age. The observed annual fluctuations in first-year growth described in

²⁵ Only the best represented age groups of the key-scale collection were included in Table 30.

the table therefore may be considered real. Further observations on the discrepancies between annual fluctuations in growth in the first and in later years of life may be found on page 275.

PROBABLE CAUSES OF FLUCTUATIONS IN THE ABUNDANCE OF YEAR
CLASSES AND IN GROWTH RATE

The obvious correlation between fluctuations in the strength of year classes and annual variations in growth rate of the Nebish Lake rock bass suggests the possibility that the two may have a common cause or may be to a certain extent interdependent. It may be seen from the data of the preceding sections that the 5-year period, 1924 to 1928, was one both of poor growth (in the second and later years of life²⁶) and of weak year classes. The remaining years for which data were available were by comparison years of relatively good growth and strong year classes. The extent of the correlation can be brought out better by the ordinal arrangement of the different calendar years with respect to the strength of year classes and growth rate.

Since the data on growth rate given in Table 27 covered the 10-year period, 1922 to 1931, and those on the abundance of year classes included the 10 years, 1921 to 1930, a comparison of annual variations will be assisted greatly if rough estimates are made of the quality of growth in 1921 and of the strength of the 1931 year class. The single comparison between growth in 1921 and 1922 (growth of females in the second year of life, Table 25) yielded the estimate that 1921 growth was 13.3 per cent below 1922 growth and hence 3.4 per cent below the 1922-1931 average. (See p. 257.) In the 11-year period, 1921 to 1931, the growth in 1921 therefore occupies sixth position. The estimate of the strength of the 1931 year class must be based entirely on its representation in the 1935 collection. From Table 23 it may be seen that the 1931 year class made up 12.9 per cent of the 1935 collection and had a representation exactly equal to that of the 1929 year class. The 1929 year class previously was given a ranking of 5 in a 10-year period (p. 248). If some allowance is made for the greater age of the 1929 year class as compared with the 1931 year class at the time of capture in 1935, the 1931 year class should be recognized to be somewhat the weaker. A

²⁶ Discussions of first-year growth may be found on p. 259.

ranking of 6 for the 1931 year class in an 11-year period possibly does not do serious violence to the truth.

If the above estimates of the growth in 1921 and the strength of the 1931 year class are accepted, the following ordinal positions of the calendar years are obtained with respect to strength of year class and growth rate. The position, 1, refers to the best growth and the strongest year class.

Position with respect to:

Year	Strength of year class	Growth rate
1923	1	4
1930	2	3
1922	3	2
1921	4	6
1929	5	5
1931	6	1
1924	7	10
1926	8	8
1925	9	7
1928	10	11
1927	11	9

The above arrangement substantiates the previous assertion that the period, 1924 to 1928, was one of poor growth and weak year classes. By comparison, growth was better and year classes were stronger in the years, 1921 to 1923 and 1929 to 1931.

Meteorological conditions may be expected to occupy an important position among the factors that contributed to the observed annual fluctuations in growth rate and the strength of year classes. Detailed tabulations were prepared of weather conditions in Vilas County²⁷ in regard to temperature, precipitation, and the percentage of possible sunshine in the six months, May to October, over the period, 1921 to 1934. Preliminary examinations revealed no correlation between annual fluctua-

²⁷ Records of the U. S. Weather Bureau (Climatological Data for the United States by Sections, Vols. VIII-XXI) were consulted for stations at Rest Lake about 14 miles (22 kilometers) to the northwest of Nebish Lake and at Big St. Germain Dam, about 10 miles (16 kilometers) to the southeast. Tabulations were based on the averages for the two stations. Occasionally defective records or a lack of records for one of the stations made it necessary to employ data from a single locality. These gaps do not affect seriously the validity of the data since the agreement between the stations ordinarily was close.

TABLE 31. Average air temperatures in °F. at two weather stations near Nebish Lake in each of 6 months over the period, 1921-1934, and the deviation of each month's temperature from the 1921-1931 average for that month.

Month	Average air temperature (°F.) in calendar year														Average for 1921-1931
	1921	1922	1923	1924	1925	1926	1927	1928	1929	1930	1931	1932	1933	1934	
May	54.8	59.0	51.6	43.5	48.5	54.6	49.5	53.4	48.5	52.9	49.4	50.6	53.8	58.0	51.4
June	67.4	61.2	66.2	58.0	62.6	57.2	58.2	56.1	59.3	62.6	62.9	63.5	67.9	65.6	61.1
July	71.5	62.8	68.2	61.5	64.5	65.1	62.4	65.8	65.4	65.6	67.0	65.2	68.0	67.7	65.4
August	63.6	63.8	59.9	61.2	66.6	63.4	58.6	63.2	62.3	65.2	61.2	63.8	60.6	61.0	62.6
September	58.4	58.6	57.0	52.6	59.3	53.2	59.8	51.6	53.8	55.8	60.2	50.2	59.7	55.0	56.4
October	46.6	47.1	43.6	51.2	35.2	41.8	46.6	44.0	44.0	43.8	47.5	39.4	40.1	47.6	44.7

Month	Departure of temperature from 1921-1931 mean in calendar year														Average for 1921-1931 ¹
	1921	1922	1923	1924	1925	1926	1927	1928	1929	1930	1931	1932	1933	1934	
May	3.4	7.6	0.2	-7.9	-2.9	3.2	-1.9	2.0	-2.9	1.5	-2.0	-0.8	2.4	6.6	3.2
June	6.3	0.1	5.1	-3.1	1.5	-3.9	-2.9	-5.0	-1.8	1.5	1.8	2.4	6.8	4.5	3.0
July	6.1	-2.6	2.8	-3.9	-0.9	-0.3	-3.0	0.4	0.0	0.2	1.6	-0.2	2.6	2.3	2.0
August	1.0	1.2	-2.7	-1.4	4.0	0.8	-4.0	0.6	-0.3	2.6	-1.4	1.2	-2.0	-1.6	1.8
September	2.0	2.2	0.6	-3.8	2.9	-3.2	3.4	-4.8	-2.6	-0.6	3.8	-6.2	3.3	-1.4	2.7
October	1.9	2.4	-1.1	6.5	-9.5	-2.9	1.9	-0.7	-0.7	-0.9	2.8	-5.3	-4.6	2.9	2.8

¹ Mean of the absolute values.

TABLE 32. Average precipitation in inches at two weather stations near Nebish Lake in each of 6 months over the period, 1921-1934, the deviation of each month's precipitation from the 1921-1931 average for that month, and the maximum 24-hour precipitation in each month.

Month	Total precipitation in calendar year														Average for 1921-1931
	1921	1922	1923	1924	1925	1926	1927	1928	1929	1930	1931	1932	1933	1934	
May	2.80	3.98	2.64	3.10	1.27	2.60	3.56	2.08	1.96	4.28	1.48	3.46	3.10	2.03	2.70
June	1.00	5.86	7.16	3.76	4.26	4.10	2.92	5.40	4.98	7.13	6.22	3.66	3.36	3.66	4.80
July	6.23	3.24	6.14	3.05	2.78	3.74	5.70	4.08	4.99	2.35	3.22	2.57	2.02	2.06	4.14
August	3.86	2.57	2.46	5.17	3.43	4.80	1.96	5.74	1.91	0.34	3.70	5.82	1.33	3.18	3.27
September	4.36	5.76	2.22	2.82	4.68	6.66	2.94	5.30	4.25	3.20	6.52	1.79	3.12	10.02	4.43
October	1.23	1.31	1.74	0.88	1.90	2.78	2.31	3.71	2.73	2.90	2.93	1.20	2.73	3.28	2.22
Month	Departure of precipitation from the 1921-1931 mean in calendar year														Average for 1921-1931 ¹
	1921	1922	1923	1924	1925	1926	1927	1928	1929	1930	1931	1932	1933	1934	
May	0.10	1.28	-0.06	0.40	-1.43	-0.16	0.86	-0.62	-0.74	1.58	-1.22	0.76	0.40	-0.67	0.76
June	-3.80	1.06	2.36	-1.04	-0.54	-0.70	-1.88	0.60	0.18	2.33	1.42	-2.26	-1.44	-1.14	1.45
July	2.09	-0.90	2.00	-1.09	-1.36	-0.40	1.56	-0.06	0.85	-1.79	-0.92	-1.57	-2.12	-2.08	1.18
August	0.59	-0.70	-0.81	1.90	0.16	1.53	-1.31	2.47	-1.36	-2.93	0.43	2.55	-1.94	-0.09	1.29
September	-0.07	1.33	-2.21	-1.61	0.25	2.23	-1.49	0.87	-0.18	-1.23	2.09	-2.64	-1.31	5.59	1.23
October	-0.99	-0.91	-0.48	-1.34	-0.32	0.56	0.09	1.49	0.51	0.68	0.71	-1.02	0.51	1.06	0.73
Month	Maximum precipitation in 24 hours in calendar year														Average for 1921-1931
	1921	1922	1923	1924	1925	1926	1927	1928	1929	1930	1931	1932	1933	1934	
May	1.06	1.32	0.80	1.08	0.41	0.76	0.89	0.98	0.82	1.24	0.44	0.89	1.16	0.55	0.89
June	0.52	1.98	2.43	0.75	0.87	1.37	1.29	0.80	2.20	2.40	1.32	0.70	0.97	1.08	1.45
July	2.20	1.02	1.15	0.70	0.96	0.70	1.40	1.57	1.80	0.80	0.85	0.95	1.29	0.76	1.20
August	1.10	1.12	0.88	2.30	1.85	1.85	0.94	1.42	0.62	0.30	1.40	2.98	0.70	1.05	1.25
September	2.23	2.17	0.88	1.12	1.60	1.96	0.95	2.47	1.60	1.08	1.30	0.50	1.02	2.41	1.58
October	0.60	0.68	0.80	0.31	0.80	1.16	1.20	1.00	1.20	1.30	0.60	0.42	0.73	1.50	0.88

¹ Mean of the absolute values.

tions in the percentage of possible sunshine and growth or the strength of year classes; consequently no data on sunshine are presented here. Tables 31 and 32 contain records of temperature and rainfall.

It is realized that records of fluctuations in air temperature do not by any means provide a precise measure of fluctuations in water temperature. Nevertheless, water temperatures of a small, relatively shallow lake may be expected to vary in the same direction as air temperatures.

The examination of Table 31 reveals that in general the years in which growth was good and strong year classes were produced tended to have temperature above the average. On the other hand the total precipitation for the 6-month period (Table 32) does not appear to be correlated with either growth or the strength of the year classes. The data for the individual months, however, show that the early-season (May, June, and July) rainfall tended to be above average in the years of good growth and strong year classes. It is particularly noteworthy that the two years with exceptionally rich year classes (1923 and 1930) had especially heavy rainfall in June. Precipitation was above average also in July, 1923, and in May, 1930. The temperature deviations for the early season, especially for June, indicate that the correlation between high temperatures in the season as a whole and growth and the strength of year classes may result largely from the high temperatures in the early part of the summer. It appears valid to conclude, therefore, that the Nebish Lake rock bass tended to grow more rapidly and produce stronger year classes in those years in which the early season had heavy rainfall and temperatures above the average.

There are, to be sure, certain exceptions to the trends outlined in the preceding paragraph. For example, 1921, a year in which growth was only slightly below average and which was estimated to have given rise to a fairly strong year class, nevertheless had such a deficiency of rainfall in June that the early season must be characterized as dry. However, the exceptions that occur do not appear to invalidate the belief that good growth and strong year classes were associated with high temperatures and heavy precipitation in the early season.

In an attempt to obtain more complete information on possible relationships between meteorological conditions and fluctuations in growth and the strength of year classes, a series of computations was made of coefficients of correlation based on annual deviations of growth, abundance, temperature, and rainfall from the mean for the 11 years, 1921 to 1931. With the year classes, the ordinal arrangement of the years (p. 263) was taken as representative of relative abundance. Admittedly a more precise evaluation of the strength of the year classes would have been desirable. It was not believed, however, that the original data were sufficiently reliable to make the (necessarily) arbitrary assignment of weights valid.

Table 33 shows the coefficients of correlation between growth and the strength of year classes of Nebish Lake rock bass and meteorological conditions (deviations from average temperature and rainfall) over the period, 1921 to 1931, for each of six months and for certain groupings of months. (The data for the Muskellunge Lake rock bass will be discussed on p. 276.) If a probability of 0.95 or greater that a correlation exists is accepted as indicative of significance, the smallest significant (absolute) value of the coefficient is 0.60.²⁸

The coefficients of correlation of Table 33 support the earlier statement that good growth and strong year classes are associated with high temperatures and heavy rainfall in early season. With a single exception (the correlation between July precipitation and growth) the coefficients were all positive for the first three months. However, only 1 of the 12 coefficients had a value in excess of 0.60 (correlation between June temperature and the strength of the year classes). In the late-season data none of the coefficients exceeded the absolute value of 0.60. The strongest indicated correlations were the positive correlation ($r = 0.55$) between September temperature and growth and the negative correlations between August precipitation and growth ($r = -0.48$) and the strength of year classes ($r = -0.50$).

The general failure of meteorological conditions in the indi-

²⁸ If the value of t corresponding to a probability of 0.05, when the number of degrees of freedom (n) is 9, is substituted in the formula, $t = \frac{r\sqrt{n}}{\sqrt{1-r^2}}$, the value of r is 0.602. See Goulden (1939) or other of the recent textbooks on statistical methods.

TABLE 33. Coefficients of correlation (r) between the annual fluctuations in the growth and in the strength of the year classes of the rock bass of the Nebish and Muskellunge lakes and the annual fluctuations in temperature or precipitation in certain months and combinations of months.

Month or months	Nebish Lake				Muskellunge Lake			
	Growth		Strength of year class		Growth		Strength of year class	
	Temperature	Precipitation	Temperature	Precipitation	Temperature	Precipitation	Temperature	Precipitation
May	0.20	0.05	0.33	0.36	0.32	0.14	0.30	0.25
June	0.54	0.56	0.69	0.45	0.75	-0.06	0.32	0.17
July	0.24	-0.22	0.43	0.08	0.47	0.29	0.38	0.30
August	-0.01	-0.48	0.10	-0.50	0.12	-0.18	0.13	0.05
September	0.55	0.21	0.12	-0.24	0.31	-0.11	-0.31	-0.35
October	0.12	-0.01	0.17	-0.31	0.23	-0.66	0.06	-0.21
All six months	0.56	0.12	0.62	-0.05	0.74	-0.23	0.33	0.13
May and June	0.47	0.51	0.64	0.56	0.67	0.01	0.46	0.27
May and July	0.44	0.40	0.62	0.52	0.68	0.16	0.37	0.41
May, June, and July	0.43	0.37	0.62	0.62	0.66	0.20	0.47	0.47
July and August	0.17	-0.52	0.37	-0.34	0.42	0.06	0.36	0.24
June and September	0.61	0.57	0.47	0.20	0.61	-0.12	0.03	-0.09
May, June, July, and September	0.53	0.55	0.55	0.47	0.65	0.13	0.29	0.22
August, September, and October	0.53	-0.16	0.31	-0.48	0.53	-0.35	-0.11	-0.22

vidual months to exhibit definitely significant correlations with annual fluctuations in growth and the strength of year classes should not be taken as proof that temperature and rainfall did not have a significant effect on these two phases of the life history of the Nebish Lake rock bass. It is possible—indeed, reasonably may be expected—that growth and the abundance of year classes may be affected more by conditions over a period of 2 or more months than by conditions in any single month. To test this possibility coefficients of correlation were computed between growth and abundance and weather conditions in eight groups of months (see lower part of Table 33). The coefficients for these combinations of months provide much stronger evidence that weather conditions in certain limited periods may have an important effect on annual fluctuations in growth and abundance.

The coefficient of correlation between temperature and growth did not exceed 0.60 for any single month and was below this value for all but one of the groups of months. The total temperature deviation for June and September did, however, exhibit a significant correlation with growth ($r = 0.61$). This apparent effect of temperature fluctuations on annual differences in growth rate may depend on a control of the length of the growing season. In the light of the observations on the course of growth during the season (p. 290), it is not unreasonable to expect that cold weather in June and September may cause the period of active growth to be shorter than usual, and that warm weather in these two months may lead to a relatively long growing season.

The coefficient of correlation between growth and precipitation did not exceed 0.60 for any of the groupings of months but the values were consistently positive for those groups of months that included June. The oligotrophic nature of Nebish Lake gives good cause to expect beneficial effects from heavy early-season rainfall. Where the natural supply of organic materials and nutrient salts is so scanty, the quantity of materials washed in during the course of a heavy downpour²⁹ well may bring about

²⁹ Comparisons of total precipitation and the maximum precipitation in a 24-hour period (Table 32) reveal that ordinarily the months with a high total precipitation also experienced heavy falls of rain within short periods.

a significant enrichment of the lake. Materials added in early season should be more completely available for utilization than substances washed in during the later months. It is true that the coefficient of correlation between growth and precipitation in June and September was fairly high ($r = 0.57$). However, the correlation with precipitation in June alone was almost equally strong ($r = 0.56$) whereas the correlation between growth and precipitation in September alone was weak ($r = 0.21$). A negative correlation existed between growth and rainfall for the two periods, July and August, and August, September, and October. The absolute values of the coefficients were both less than 0.60. For further discussion of these negative coefficients see p. 273.

High temperatures, especially in early season, show a decidedly positive correlation with the strength of the year classes. The coefficients of correlation were greater than 0.60 for June and for four of the eight groupings of months. No month or combination of months showed a negative correlation between temperature and the strength of year classes. High temperatures possibly may improve food conditions for and thus promote a greater survival of young fish.

The high correlation between June temperatures and the strength of year classes suggests the possibility that the relative abundance of year classes of the Nebish Lake rock bass may be determined by the rate of survival very early in the life of the individuals. The exact time of spawning and hatching of the Nebish Lake rock bass is not known, but the absence of any maturing or ripe fish in a collection taken July 5 and 6, 1930, provides evidence that most if not all of the eggs are deposited and that at least part of the development of the eggs occurs during June.³⁰

³⁰ A deposition of the eggs much earlier than June is most unlikely, since the ice does not disappear from the lakes until "about the first of May" (Juday and Birge, 1930). In Lake Maxinkuckee (northern Indiana) where the ice usually disappears in the latter part of March the rock bass begin to spawn "about the middle of May and are usually done by June 15" (Evermann and Clark, 1920). In northern New York, where climatic conditions are more nearly comparable with those in northeastern Wisconsin, Greeley (1930) found two nests containing eggs in the Big Chazy River (Champlain watershed) on July 9. However, the eggs already had hatched on July 2 in a nest located in a tributary of this same stream. Greeley and Greene (1931) found a "nest with eggs and a male on guard" on Tibbits Creek (St. Lawrence watershed) on June 5.

Although the coefficients of correlation between precipitation and the strength of the year classes were positive for May and June and for all groupings that included these months, only one coefficient exceeded 0.60 (correlation between strength of year class and precipitation in May, June, and July; $r = 0.62$). This value constitutes evidence for a beneficial effect of heavy early-season rainfall on the survival of young. The most logical explanation of such a relationship appears to lie in the assumption that materials washed in during the early season bring about an improvement in feeding conditions for and consequently a greater survival of the young fish.

The coefficients of correlation between late-season precipitation and the strength of year classes were all negative but had (absolute) values less than 0.60. Two of the eight groupings also had negative coefficients.

Attention should be called to the existence of a factor that complicates the interpretation of the data of Table 33, namely, the apparent correlation of growth and the abundance of year classes with both temperature and precipitation. For example, there is evidence that growth is correlated positively with June temperature and precipitation. Now if June temperature and precipitation are correlated negatively or vary independently the values of r in Table 33 are too low. If, on the other hand, June temperature and precipitation have a strong positive correlation the values of r in Table 33 may be held to represent, to a certain extent, the combined effects of the two phases of the weather and are therefore too high. The actual computation of the correlation between June temperature and rainfall yielded a value of $r = 0.01$. If partial coefficients of correlation are computed, the following results are obtained: The correlation between June temperature and growth, with rainfall held constant is 0.64; the correlation between June rainfall and growth, with temperature held constant is 0.65. Both of these values are slightly above the lowest significant value, 0.63.³¹

Table 34 shows partial coefficients of correlation computed from the above and from several other combinations of data. The partial coefficients of correlation of growth and meteorologi-

³¹ The computation of the partial coefficient of correlation involves the loss of one degree of freedom; consequently a higher value of r is necessary to obtain a value of t corresponding to a probability of 0.05.

TABLE 34. *Partial coefficients of correlation between the annual fluctuations in growth and in the strength of the year classes of the Nebish Lake rock bass and the annual fluctuations in weather conditions in certain months and combinations of months.*

Biological variable	Variable meteorological factor	Meteorological factor held constant	r
Growth	Temperature (June)	Precipitation (June)	0.64
do.	Precipitation (June)	Temperature (June)	0.65
do.	Temperature (June and September)	Precipitation (June)	0.76
do.	Precipitation (June)	Temperature (June and September)	0.73
do.	Temperature (June and September)	Precipitation (August)	0.50
do.	Precipitation (August)	Temperature (June and September)	-0.29
Abundance	Temperature (June)	Precipitation (June)	0.76
do.	Precipitation (June)	Temperature (June)	0.60
do.	Temperature (June)	Temperature (May, June, and July)	0.72
do.	Precipitation (May, June, and July)	Temperature (June)	0.66
do.	Precipitation (May, June, and July)	Precipitation (August, September, and October)	0.50
do.	Precipitation (August, September, and October)	Precipitation (May, June, and July)	-0.26
do.	Temperature (June)	Precipitation (August, September, and October)	0.61
do.	Precipitation (August, September, and October)	Temperature (June)	-0.26

cal conditions based on June precipitation and temperatures in June and September are considerably higher than those based on June weather alone. With June rainfall held constant, the coefficient of correlation between growth and temperature in June and September is 0.76. When the temperature in these two months is held constant the coefficient of correlation of growth with June precipitation is 0.73. The value, -0.29 , for the coefficient of correlation between August precipitation and growth, with the June and September temperature held constant gives evidence that the greater negative simple coefficient (-0.48) between August precipitation and growth depended in large measure on the fact that the years with high June and September temperatures had a deficiency in rainfall in August. On purely mathematical grounds it might be argued, of course, that the high simple correlation between growth and June and September temperature ($r = 0.61$) depended in part on the deficiency in August rainfall in the years with high temperatures in these two months. However, it is difficult to conceive in what manner heavy August rainfall might impede the growth of the rock bass in Nebish Lake. In some lakes the increased turbidity that follows heavy rainfall may bring about a reduction in the growth of plankton. Nebish Lake, however, is not subject to high turbidity resulting from heavy precipitation. The soil of the surrounding land is sandy and is covered by a relatively dense growth of vegetation. On the other hand a connection between growth and June and September temperature has a sound biological explanation (p. 269).

Significant partial coefficients of correlation between the strength of year classes and June temperatures were obtained with precipitation held constant in June ($r = 0.76$) and in May, June, and July ($r = 0.72$). The coefficient of correlation between the abundance of year classes and precipitation in May, June, and July, with June temperature held constant ($r = 0.66$) also was above 0.63. None of the remaining partial coefficients had significant values. The partial coefficients of correlation between the strength of year classes and late-season (August, September, and October) precipitation, with early-season (May, June, and July) precipitation held constant, ($r = -0.26$) and with June temperature held constant ($r = -0.26$) have consid-

erably smaller negative values than the simple correlation between late-season rainfall and abundance ($r = -0.48$). It is believed that the negative correlation between late-season precipitation and abundance is the result of a late-season deficiency in rainfall in those years in which early-season conditions were conducive to the production of strong year classes.

The data that have been presented and discussed in the preceding pages appear to make valid the conclusion that annual fluctuations in both the growth and the strength of the year classes of the Nebish Lake rock bass are correlated significantly with annual variations in temperature and rainfall. Growth is correlated more closely with temperature in June and September and rainfall in June than with conditions in other months. The strength of the year classes seems to be correlated most closely with early-season (May, June, and July) temperature and rainfall, with June conditions more important than those for other months.

The small amount of information on the growth of the Nebish Lake rock bass beyond 1931 (Table 28) makes it possible to form some judgment as to whether the relationships observed for the 11 years, 1921 to 1931, hold for growth in later years. From Table 31 it may be seen that early-season (particularly June) temperatures were not greatly different in 1931 and 1932. September temperatures, however, were lower by 10.0° F. in the latter year. Comparisons of rainfall (Table 32) show 1932 to have had a drier early season than 1931. On the basis of the low temperatures in September and the early-season deficiency in rainfall, growth in 1932 would be expected to be poorer than growth in 1931. This expectation is in agreement with the facts; growth declined from 20.6 per cent above the 1922-1931 average in 1931 to 4.8 per cent above average in 1932.

The deficiency in precipitation that characterized the early season of 1932 continued through 1933 and 1934. However, the data on temperature fluctuations in June and September give cause to expect an improvement in growth in 1933, followed by a decline in 1934. The improvement did not occur in 1933; on the contrary the deviation from average growth declined slightly (from 4.8 per cent in 1932 to 4.0 per cent in 1933). The expected decline did occur in 1934 (from 4.0 per cent in 1933 to

—9.9 per cent in 1934). The relationship between growth and weather conditions in the years, 1932 to 1934, cannot be said to lend strong support to or to be seriously incompatible with the belief that high June and September temperature and heavy early-season precipitation are conducive to good growth. Predictions based on the examination of meteorological data were accurate for two of the three years.

The preceding discussion has been concerned with the effects of only two factors, temperature and precipitation, on annual fluctuations in the growth and the strength of the year classes of the Nebish Lake rock bass. Recognition must be given also to certain biological factors of possibly great importance. In late summer at least, the Nebish Lake rock bass lives in rather close association with perch and smallmouth black bass. Since the three species are to a large degree competitors for food in Nebish Lake (Couey, 1935) large fluctuations in the abundance of any one species probably affect the abundance and growth of the other two species.

Fluctuations in the strength of year classes of the rock bass itself possibly may be reflected in the survival of young and in the growth rate in later years. For example, the great abundance of rock bass that must have existed for several years following the production of the extremely rich 1923 year class may well have contributed to the slow growth and poor survival of young during the period, 1924 to 1928. Furthermore, it is readily conceivable that five consecutive years of poor survival may have reduced the population density sufficiently to permit the observed improvements in survival and growth rate following 1928. Finally, the production of a second exceptionally strong year class in 1930 was followed by a decline in growth rate that began in 1932 and continued at least 2 more years. These considerations seem to throw a justifiable doubt on the biological significance of the statistically significant correlation between meteorological conditions and the fluctuations in the growth and the strength of the year classes of the Nebish Lake rock bass.

Mention should be made also of the fact that first-year growth does not appear to be correlated with either temperature or precipitation. Obviously, the conditions that control the rate of growth in the first year and in the later years of life are not

the same. The first-year rock bass failed entirely to share the improvement in the growth of older fish over the period, 1929 to 1931. In 1931 when the growth of fish in the second and later years of life was at the maximum the young of the year grew more slowly than in any other year of the period, 1920 to 1931 (Tables 27 and 29). Furthermore, the growth of first-year fish reached a maximum in 1924 when the growth of older fish was unusually slow.

The discussion of this section has placed emphasis on the correlation between fluctuations in the strength of year classes and in growth in the second and later years of life. It would be more logical to expect a correlation between first-year growth and survival of young fish. However, such a correlation does not exist. It is true that first-year growth was above average in 1923 when a phenomenally strong year class was produced. On the other hand, members of the strong 1930 year class grew poorly in their first year. Furthermore, the year of maximum first-year growth (1924) gave rise to a relatively weak year class. The lack of correlation between first-year and later growth may be due to the occupancy of different habitats and the consumption of different foods by young of the year and older fish. The lack of correlation between first-year growth and the survival of young is more difficult to explain. It can be said only that the factors that control these two phases of the early life history of the rock bass appear not to be the same. It can be stated also that the abundance of the young of the year does not seem to affect first-year growth.

Information on the annual fluctuations in growth and the strength of year classes of rock bass in Muskellunge and Silver Lakes makes possible a brief examination of the relationship between meteorological conditions and these two phases of the life history of the rock bass in two additional populations.³² Attention will be given first to the data for the rock bass of Muskellunge Lake.

³² The information that will be presented here on the growth and the strength of the year classes of the rock bass of Muskellunge and Silver Lakes has not been based on all available collections. However, the date of completion of the age and growth studies of these two rock bass populations is most indefinite; consequently it has been considered desirable to make use of those portions of the data that are applicable to problems considered in this paper.

TABLE 35. Annual increments of growth in length (in millimeters) of the males of the various year classes of the Muskellunge Lake rock bass.

Year of life	Calendar year											Unweighted mean
	1921	1922	1923	1924	1925	1926	1927	1928	1929	1930	1931	
11	..	..	..	..	..	..	..	..	..	..	6	6
10	..	..	..	..	..	..	..	..	..	7	7	7
9	..	..	..	..	..	..	..	..	..	11	13	11
8	..	..	..	..	..	..	..	..	..	16	15	13
7	..	..	..	..	..	..	..	..	..	19	15	17
6	..	..	..	..	..	..	..	..	..	18	15	17
5	..	..	..	..	..	..	..	..	..	20	18	17
4	..	..	..	..	..	..	..	..	..	24	21	21
3	..	..	..	..	..	..	..	..	..	17	18	19
2	..	..	..	..	..	..	..	..	..	21	21	19
1	..	..	..	..	..	..	..	..	..	15	22	19
37	..	34	34	35	33	30	30	31	32	17	..	19
Number of fish taken in year	..	9	18	6	3	..	..	..	..	..	..	36
1930	3	20	53	16	18	18	4	..	..	..	..	132
1931	2	3	9	3	1	4	3	14	12	..	..	51
1932	5	32	80	25	22	22	7	14	12	..	..	219
Total												

¹ Represented by only one fish.

TABLE 36. Annual increments of growth in length (in millimeters) of the females of the various year classes of the Muskellunge Lake rock bass.

Year of life	Calendar year											Unweighted mean
	1921	1922	1923	1924	1925	1926	1927	1928	1929	1930	1931	
10	..	..	..	..	..	..	..	..	..	9	9	9
9	..	..	..	..	..	..	..	..	10	10	9	10
8	..	..	..	..	..	..	..	9	11	14	12	12
7	..	..	..	..	..	..	10	12	18	18	13	14
6	..	..	..	..	..	15	17	14	18	18	18	17
5	..	..	..	..	..	18	15	16	22	16	1..	18
4	..	..	..	..	21	18	19	15	19	16	20	19
3	..	..	..	21	16	16	15	19	20	17	20	18
2	..	21	19	17	17	16	17	22	21	19	..	19
1	35	34	33	32	33	30	28	30	30	..	..	32
Number of fish taken in year Total	7	16	27	21	14	..	..	..	..	..	..	85
	18	27	68	6	20	13	8	..	..	..	..	160
	..	4	10	9	4	4	1	20	13	..	..	65
	25	47	105	36	38	17	9	20	13	..	..	310

¹ Represented by only one fish.

Tables 35 and 36 show the growth increments of the Muskellunge Lake rock bass according to calendar year and year of life. These data were analyzed by the same methods described for the Nebish Lake material. The annual fluctuations in growth are recorded in Table 37. In the Muskellunge Lake data as in the Nebish Lake data the indicated deviation of the 1921 growth (Table 39) from the 1922-1931 average must be considered a rough estimate.³³

TABLE 37. *Deviation of the growth of the Muskellunge Lake rock bass in different calendar years from the average for the 10-year period, 1922 to 1931. (First-year growth was excluded from the computations.)*

Sex	Percentage deviation from average growth in calendar year									
	1922	1923	1924	1925	1926	1927	1928	1929	1930	1931
Male	24.8	19.9	7.2	3.6	-14.8	-19.3	-18.3	3.4	-7.4	1.1
Female	22.5	12.5	-3.3	-6.9	-14.0	-14.0	-8.8	9.8	1.6	0.6
Average	23.6	16.2	2.0	-1.6	-14.4	-16.6	-13.4	6.6	-2.9	0.8

The age and year-class composition of the rock bass collected from Muskellunge Lake in six calendar years may be seen in Table 38. The records for 1927 and 1928 were taken from Wright's (1929) paper (Wright's method of designating age has been modified to conform with the method used in this paper). The remaining data are presented here for the first time.

The estimate of the ordinal ranking of the calendar years as to strength of the year classes of the Muskellunge Lake rock bass given in Table 39 (the rating, 1, designates the strongest year class) was made from the examination of Table 38. The basis for the rankings will be discussed only briefly and for only a few year classes. The 1923 year class was considered the strongest in the 11-year period because of its dominance as age-groups V, VII, and VIII, and its strength as age-group IX. No significance can be attached to the scarcity of the 1923 year class as age-group IV in the 1927 collections. Although Wright (1929) gave

³³ Since only three specimens were available, the data on the growth of the 1920 year class of the Muskellunge Lake rock bass were not employed in the computation of fluctuations in growth over the period, 1922 to 1931 and hence were omitted from Tables 35 and 36. The single male specimen had a second-year growth (in 1921) that was 25 per cent above the 1923 level. The 1921 growth of the two females was 4.9 per cent below 1922 growth. The (weighted) mean percentage was 5.1 and hence the 1921 growth was 5.1 per cent above 1922 growth or $5.1 + 23.6 = 28.7$ per cent above the 1922-1931 level.

TABLE 38. Numerical and percentage representation of the year classes of the Muskellunge Lake rock bass in the different years' collections and for all collections combined. (Data for 1927 and 1928 taken from the publication by Wright, 1929).

Year of capture	Item	Year Class																Total
		1917	1918	1919	1920	1921	1922	1923	1924	1925	1926	1927	1928	1929	1930	1931	1932	
1927	Age group Number of fish Percentage	X 2 1.8	IX 6 5.5	VIII 9 8.2	VII 21 19.1	VI 45 40.9	V 25 22.7	IV 2 1.8	..	..	..	..	..	..	..	..	..	110
1928	Age group Number of fish Percentage	..	..	IX 3 2.3	VIII 21 16.3	VII 36 27.9	VI 29 22.5	V 38 29.5	..	III 2 1.5	..	..	..	..	..	..	..	129
1930	Age group Number of fish Percentage	..	..	XI 1 0.7	X 1 0.7	IX 7 5.0	VIII 25 17.7	VII 45 31.9	VI 27 19.1	V 17 12.1	IV 8 5.7	III 10 7.1	..	..	..	..	..	141
1931	Age group Number of fish Percentage	..	..	..	XI 2 0.5	X 20 5.0	IX 45 11.2	VIII 120 29.8	VII 21 5.2	VI 37 9.2	V 29 7.2	IV 22 5.4	III 107 26.5	..	..	..	..	403
1932	Age group Number of fish Percentage	..	..	..	..	XI 2 1.7	X 7 6.1	IX 19 16.5	VIII 12 10.4	VII 5 4.4	VI 8 7.0	V 3 2.6	IV 34 29.6	III 25 21.7	..	..	..	115
1935	Age group Number of fish Percentage	..	..	..	..	..	XIII 1 1.2	..	XI 1 1.2	..	IX 2 2.5	VIII 4 4.9	VII 31 38.3	VI 14 17.3	V 22 27.2	IV 3 3.7	III 3 3.7	81
All collections	Number of fish Percentage	2 0.2	6 0.6	13 1.3	45 4.6	110 11.2	132 13.5	224 22.9	61 6.2	61 6.2	47 4.8	39 4.0	172 17.6	39 4.0	22 2.3	3 0.3	3 0.3	979

no information as to the mesh sizes he employed, he mentioned that his nets did not take adequate samples of age-group IV and questioned the complete reliability of his V-group samples. The year class of 1928 was considered the second strongest because of its dominance in 1932 as age-group IV and in 1935 as the VII-group and its great strength in 1931 as age-group III. The estimates of the strength of the remaining year classes were based on similar considerations. A specific statement probably should be made of the reason for the assignment of the lowest ranking to the 1931 year class. The estimate of the strength of this year



FIGURE 12. Annual percentage deviation of the growth (beyond the first year) of the Nebish Lake and the Muskellunge Lake rock bass from the 1922-1931 average and of the Silver Lake rock bass from the 1926-1930 average. Solid line Nebish Lake, broken line Muskellunge Lake, dotted line Silver Lake. The deviations represent the averages of the values for both sexes.

class of the Nebish Lake rock bass was made difficult by the lack of exact information as to the mesh sizes of the gill nets employed in taking the sample (p. 248). It is known, however, that the gill nets employed for the capture of the 1935 collection from Muskellunge Lake included six different mesh sizes (all of those listed on p. 194 except the 1 $\frac{1}{4}$ -inch mesh). Nets of all seven mesh sizes were fished in Muskellunge Lake in 1931 but the 1 $\frac{1}{4}$ -inch mesh net was omitted in 1932 as well as in 1935. The nets fished in 1935, therefore, could have taken greater numbers of IV-group rock bass had they been present in abundance.

Comparisons of the annual fluctuations in growth and the strength of the year classes of the rock bass of Muskellunge and Nebish Lakes (Table 39, Fig. 12) fail to reveal an extremely close agreement between the variations in the two populations. It is true that the data agreed in 7 of 11 years as to whether growth was above or below the 1922-1931 average. Nevertheless, the actual extent of the variations in the several years differed so greatly that the correlation between the annual fluctuations in the growth of the populations was relatively low ($r = 0.38$). The low value of the coefficient may be traced particularly to disagreements as to growth in 1921 and 1931. Had more reliable data been available on growth in 1921, a higher value of r possibly might have been obtained.

The two stocks showed better agreement in the fluctuations in the strength of year classes. The most serious disagreement

TABLE 39. *Comparisons of the annual percentage deviations from 1922 to 1931 average growth and of the strength of the year classes (1 designates the strongest year class) in Muskellunge and Nebish Lakes, 1921 to 1931.*

Year	Deviation from 1922-1931 growth		Strength of year class	
	Muskellunge Lake	Nebish Lake	Muskellunge Lake	Nebish Lake
1921	28.7	-3.4	3	4
1922	23.6	8.6	4	3
1923	16.2	6.2	1	1
1924	2.0	-9.1	6	7
1925	-1.6	-4.4	8	9
1926	-14.4	-4.9	9	8
1927	-16.6	-8.1	10	11
1928	-13.4	-15.2	2	10
1929	6.6	-1.9	7	5
1930	-2.9	8.4	5	2
1931	0.8	20.6	11	6

occurred in 1928 in which year the second strongest year class in 11 years was produced in Muskellunge Lake and the second weakest was produced in Nebish Lake. The correspondence was poor also in 1930 and 1931. The correlation between the rankings in the two stocks was fairly high ($r = 0.56$) but by no means of certain significance.

The annual fluctuations in the growth of the Muskellunge Lake rock bass exhibit a strong positive correlation with fluctuations in temperature (Table 33). The value of the correlation coefficient was high for June ($r = 0.75$) and also was positive for every other month. Furthermore, the value of r exceeded 0.60 for six of the eight groupings of months.

With the exception of the large negative value of the coefficient for October ($r = -0.66$) there is little evidence for a correlation between precipitation and the growth of the Muskellunge Lake rock bass. There is reason to believe, however, that this apparently significant negative correlation between October rainfall and the growth of the Muskellunge Lake rock bass may depend on the circumstance that warm seasons were deficient in October precipitation. The coefficient of correlation between October rainfall and June temperatures was found to be -0.42 .

There is no evidence for a significant correlation between the strength of the year classes of the Muskellunge Lake rock bass and annual fluctuations in temperature or precipitation. It is of particular interest that a strong year class was produced in 1928 which year had very low temperatures and only a slight excess of rainfall in June, whereas the extremely weak year class of 1931 was produced in a year in which June temperatures were above average and an excess of rainfall occurred in June.

The failure of precipitation to show significant correlation with either the growth or the strength of the year classes of the Muskellunge Lake rock bass is not surprising. Muskellunge Lake is not only several times larger than Nebish Lake but it is much richer with respect to the organic matter of the plankton and the amount of bound CO_2 in its waters (Table 1). Accordingly, the amounts of nutrient materials washed into Muskellunge Lake during periods of heavy rainfall may be expected to have relatively much less effect.

The agreement between the first-year and later growth of the rock bass was better in Muskellunge Lake than in Nebish Lake (p. 275). It should be noted, however, that data are lacking on the first-year growth of rock bass in Muskellunge Lake in 1930 and 1931, years in which the Nebish Lake data showed pronounced discrepancies between the growth of the young of the year and older fish.

With the Muskellunge Lake rock bass as with the Nebish Lake rock bass, the possible effects of the occurrence of strong and weak year classes on growth and on the survival of young in later years should not be overlooked. The production of the three relatively strong year classes of 1921, 1922, and 1923 may have produced a population density that contributed to the declining growth of 1924 and 1925, to the very poor growth of 1926, 1927, and 1928 and to the reduced strength of the 1924 year class and the extreme weakness of the year classes of 1925, 1926, and 1927. Further evidence that population density may affect the growth of the rock bass may be found in the fact that the changes in the growth of the Muskellunge Lake and Nebish Lake rock bass in 1930 agreed very poorly. The growth of the Nebish Lake rock bass improved from 1929 to 1930 whereas that of the Muskellunge Lake stock declined. Possibly this disagreement may be associated with the occurrence of the strong 1928 year class in Muskellunge Lake. However, the simultaneous occurrence of poor growth and a strong year class in 1928 is hardly compatible with an assumption that periods of poor growth and survival are the result of overpopulation following the occurrence of strong year classes in earlier years. There appear to be other factors whose effects are independent of the density of the population.

Mention already has been made of the fact that a strong year class of the Muskellunge Lake rock bass was produced in 1928, a year that gave rise to a very weak year class of the Nebish Lake rock bass. The possibility that conditions in Muskellunge Lake in 1928 may have been favorable for the survival of the young of other species as well is suggested by the fact that the 1928 year class of the Muskellunge Lake cisco also was one of unusual strength (Hile, 1936a). It is of special interest that strong year classes occurred simultaneously in species that

spawn in the autumn³⁴ (cisco) and early summer (rock bass). Certain other observations on the cisco suggest the existence of unusual conditions in Muskellunge Lake in 1928. The calculated first-year lengths of the 1928 year class of the cisco had a distinctly bimodal distribution (Hile, 1936a), and morphometric studies (Hile, 1936b, 1937) reveal that the 1928 year class of the Muskellunge Lake cisco exhibited pronounced deviations from the normal morphological characteristics of the population. What the unusual conditions were is not known.

There are resemblances between the annual fluctuations in the growth of the rock bass and cisco³⁵ in Muskellunge lake (Table 40). The growth of both species declined in 1926. In 1927 the growth of the cisco improved slightly but that of the rock bass declined still further. The species agreed, however, in showing improved growth in 1928 and 1929, followed by a new decline in 1930. The decreased growth rate of the Muskellunge Lake rock bass in 1930 was in disagreement with the improvement in the growth of the Nebish Lake rock bass in the same year.

TABLE 40. *Comparison of the annual fluctuations (estimated percentage deviations from average) in the growth of rock bass and ciscoes in Muskellunge Lake.*

Species	Calendar year					
	1925	1926	1927	1928	1929	1930
Rock bass	—1.6	—14.4	—16.6	—13.4	6.6	—2.9
Cisco	10.2	—7.4	—3.2	1.4	9.1	—13.0

The data on the fluctuations of the growth (Tables 41, 42, and 43) and the strength of the year classes (Table 44) of the Silver Lake rock bass are relatively scanty and cover a limited period of years. At best they can be held as only roughly descriptive of the true changes that occurred.³⁶

³⁴ The year classes of the cisco are considered to originate in the year of the spring in which the eggs hatch.

³⁵ The data on the growth of the cisco have been taken from Hile (1936a). Because of differences in the period of years included in the data for the two species and in the method of computation of the percentages, attention should be given to the direction and relative extent of the changes rather than to the actual values of the percentages.

³⁶ Nearly all of the Silver Lake specimens were taken by hook and line, a method of collection less satisfactory than the use of gill nets. Small hooks were used in an attempt to minimize selection.

TABLE 41. *Annual increments of growth in length (in millimeters) of the males of four year classes of the Silver Lake rock bass.*

Year of Life	Calendar year						Unweighted mean
	1925	1926	1927	1928	1929	1930	
6	..	..	..	..	..	22	22
5	..	..	..	..	29	33	31
4	..	..	..	19	32	27	26
3	..	..	19	15	20	28	20
2	..	16	16	17	21	..	18
1	32	30	28	29	..	..	30
Number of fish taken in year } Total	1930	25	2	..	..	..	27
	1931	5	4	2	18	..	29
		30	6	2	18	..	56

TABLE 42. *Annual increments of growth in length (in millimeters) of the females of four year classes of the Silver Lake rock bass.*

Year of life	Calendar year						Unweighted mean
	1925	1926	1927	1928	1929	1930	
6	..	..	..	..	..	20	20
5	..	..	..	..	28	25	26
4	..	..	..	17	26	28	24
3	..	..	18	16	20	26	20
2	..	17	14	18	21	..	18
1	31	31	26	29	..	..	29
Number of fish taken in year } Total	1930	29	3	..	..	..	32
	1931	21	9	13	20	..	63
		50	12	13	20	..	95

The annual fluctuations in the growth of the Silver Lake rock bass (Table 43, Fig. 12) bear a general resemblance to the changes that occurred in the growth of the Nebish Lake rock bass. Both stocks had a decreasing growth rate from 1926 to a minimum in 1928, followed by pronounced improvements in growth in 1929 and 1930. The improvement in growth in 1930 is in disagreement with the change that occurred in the growth of the Muskellunge Lake rock bass.

Data on the first-year growth of the Silver Lake rock bass are available for only four years (1925 to 1928). These data agree with the data on the growth in later years in showing a decline in 1927, but the improvement in first-year growth in 1928 disagrees with the change in growth in the later years of life.

The 1925 year class of the Silver Lake rock bass stands out as exceptionally strong (Table 44). In comparison, the poorly represented year classes of 1924, 1926, and 1927 may be considered relatively weak. The dominance of the 1928 year class

in the 1931 collection suggests that this year class probably was stronger than the year classes of 1926 and 1927. The general scarcity of old fish in the collections points toward the possibility of a relatively short life span for the Silver Lake rock bass and makes impossible an evaluation of the strength of year classes earlier than that of 1924.

The occurrence of a strong year class of the Silver Lake rock bass in 1925 is in disagreement with the data for both Nebish Lake and Muskellunge Lake where the 1925 year classes were relatively weak. The 1928 year class was rich in Muskellunge Lake as well as in Silver Lake but was extremely poor in Nebish Lake. The rock bass stocks of all three lakes had relatively weak year classes in 1926 and 1927. The 1924 year class apparently was weak in Silver Lake and average or slightly below average in the other two lakes.

Contrary to the situation in Muskellunge Lake, there appears to be no correlation between the fluctuations in the strength of the year classes of the rock bass and cisco in Silver Lake. Only the 1926 year class of the cisco was designated as unusually

TABLE 43. *Deviation of the growth of the Silver Lake rock bass in different calendar years from the average for the 5-year period, 1926-1930. (First-year growth was excluded from the computations.)*

Sex	Percentage deviation from average growth in calendar year				
	1926	1927	1928	1929	1930
Male	-10.5	-10.5	-19.5	16.0	24.3
Female	-0.3	-19.7	-13.6	13.5	20.0
Average	-5.4	-15.1	-16.6	14.8	22.2

TABLE 44. *Numerical and percentage representation of the year classes of the Silver Lake rock bass (sexes combined) in the 1930 and 1931 collections.*

Year of capture	Item	Year class								Total
		1921	1922	1923	1924	1925	1926	1927	1928	
1930	Age group	IX	VIII	VII	VI	V	IV	III	..	..
	Number of fish	4	1	6	1	54	6	1	..	73
	Percentage	5.4	1.4	8.2	1.4	74.0	8.2	1.4	..	..
1931	Age group	..	IX	..	..	VI	V	IV	III	—
	Number of fish	..	1	..	..	26	12	5	52	96
	Percentage	..	1.0	..	..	27.1	12.5	5.2	54.2	..
1930 and 1931	Number of fish	4	2	6	1	80	18	6	52	169
	Percentage	2.4	1.2	3.5	0.6	47.3	10.7	3.5	30.8	..

strong (Hile, 1936a). This same year class of the rock bass already has been found to have been weak. The 1929 year class of the Silver Lake cisco was considered weak; no data are available on the strength of the 1929 year class of the rock bass.

The annual fluctuations in the growth of the rock bass and cisco of Silver Lake also exhibit disagreements (Table 45). The growth of the cisco (Hile, 1936a) failed to decline sharply as did that of the rock bass in 1927 and 1928, while in 1930 the growth of the rock bass improved and that of the cisco declined. However, both species had relatively good growth in 1929.

TABLE 45. *Comparison of the annual fluctuations (estimated percentage deviations from average) in the growth of rock bass and ciscoes in Silver Lake.*

Species	Calendar year				
	1926	1927	1928	1929	1930
Rock bass	—5.4	—15.1	—16.6	14.8	22.2
Cisco	—0.7	—0.5	—1.7	7.7	—8.0

A limited amount of data on the relative abundance of the year classes is available for one more population of rock bass of the northeastern highland region. According to Wright (1929) the 1923 year class made up 31.6 per cent (30 in a total of 95) of his 1927 collection from Trout Lake and 40.3 per cent (25 in a total of 62) of his 1928 samples. The 1923 year class was therefore one of unusual strength in three of the four lakes for which data are available. The 1923 year class was represented by only six specimens in the Silver Lake collections. However, the possibility that the Silver Lake rock bass may have a short life span (p. 287) renders the significance of this small representation doubtful.

The data that were discussed in the preceding pages contained numerous agreements and also a number of discrepancies. The possible significance of certain of the observations will be summarized briefly. There can be little doubt that meteorological conditions have important effects on the life history of the rock bass in the lakes of northeastern Wisconsin, and presumably on the life histories of other species as well. These effects are at times similar in different lakes. For example, the simultaneous occurrence of an exceptionally strong 1923 year class of

rock bass in three of four lakes for which data are available can hardly be ascribed to mere chance. There must have been a common cause, and the only factor that reasonably can be assumed to have exerted such a powerful influence simultaneously in the three lakes is weather. The strong positive correlation between annual fluctuations in temperature and the growth rate of both the Nebish Lake and the Muskellunge Lake rock bass populations likewise can be interpreted as similar effects of a common cause.

There is evidence, on the other hand, that at times conditions peculiar to individual lakes may cause weather conditions to have dissimilar effects in different bodies of water and/or that strictly local influences may be sufficiently strong to obscure or overshadow the effects of meteorological conditions. For example, the fluctuations in the growth of both the Nebish Lake and the Muskellunge Lake rock bass stocks exhibited strong positive correlation with temperature fluctuations; however, the growth fluctuations of the two stocks were correlated weakly with each other. The production in 1928 of a weak year class of the Nebish Lake rock bass and of a strong year class of the Muskellunge Lake rock bass (possibly of the Silver Lake rock bass also) must be interpreted as evidence that, in some years at least, local conditions play a dominant rôle in their effects on the life history of the species. The simultaneous occurrence in 1928 of strong year classes of the Muskellunge Lake rock bass and cisco indicates that conditions within that lake were then conducive to the survival of more than one species. In Silver Lake, however, the years of occurrence of strong year classes of the rock bass and the cisco were not the same.

In Nebish Lake the annual fluctuations in first-year growth showed little correlation with the fluctuations in growth in the later years of life. The less extensive data for the rock bass of Muskellunge Lake suggest that the fluctuations in the first-year growth of the rock bass in that lake agreed somewhat more closely with the fluctuations in the growth of older fish.

A continuation of this discussion would contribute little toward the clarification of the general problem of the causes underlying the observed annual fluctuations in the growth and the strength of the year classes. The problem must be recognized as

exceedingly complex. Continued investigations over a period of years doubtless would contribute much to an improved understanding of certain phases of the problem. To be most effective these studies should be conducted simultaneously on a number of lakes, should give consideration to the biology of all important species in each lake, and should have the support of concurrent intensive limnological investigations.

PERCENTAGE OF THE SEASON'S GROWTH IN LENGTH COMPLETED AT THE TIME OF CAPTURE

The routine of field operations, which involved the collection of a variety of species from a number of lakes, made it impossible to trace the progress of the growth of the Nebish Lake rock bass through the summer by means of collections taken at intervals throughout the growing season. It is possible, however, to estimate the percentage of the total season's growth that fish of certain age groups had completed up to the time of capture. The procedure consists of a comparison of the calculated length increment for that part of the growing season preceding capture with the length increment for the entire season as calculated from samples of the same year class taken in subsequent calendar years.³⁷ The following examples will illustrate the method.

The calculated growth in 1930 of the VII-group males of the 1930 collection up to the time of capture, August 16 to 21, was 6 millimeters (Table 46). Fish of the same (1923) year class appeared in the 1931 collection as age-group VIII and in the 1932 collection as age-group IX. The total 1930 growth of the 1923 year class was determined as 8 millimeters from each of these later collections. The VII-group males of the 1930 collection therefore had completed 75 per cent of their season's growth at the time they were captured. The female rock bass of the same age grew 4 millimeters in 1930 before capture. The total 1930 growth was determined as 7 millimeters from the 1931 VIII-group and as 6 millimeters from the 1932 IX-group. The percentage of growth completed before capture was $100 \times \frac{4}{6.5}$ or 61.5.

³⁷ Comparisons must be based on successive samples of the same year class in order to avoid the possible distorting effects of fluctuations in growth rate in different calendar years.

TABLE 46. Comparison of the calculated growth in millimeters of five age groups of Nebish Lake rock bass in 1930 up to the time of capture, August 16 to 21, with the growth for the entire season as calculated from 1931 and 1932 collections of the same year classes. Numbers of specimens in parentheses.

Age in 1930	Males				Females			
	1930 growth up to time of capture	Total 1930 growth computed from 1931 collection	Total 1930 growth computed from 1932 collection	Percentage of year's growth completed at capture	1930 growth up to time of capture	Total 1930 growth computed from 1931 collection	Total 1930 growth computed from 1932 collection	Percentage of year's growth completed at capture
VIII	..	..	..	..	3 (8)	5 (47)	5 (33)	60.0
VII	.. 6 (15)	.. 8 (117)	.. 8 (41)	.. 75.0	4 (43)	7 (99)	6 (74)	.. 61.5
VI	..	..	..	..	6 (6)	9 (24)	6 (17)	.. 80.0
V	.. 15 (9)	.. 17 (5)	.. 18 (5)	.. 85.7	13 (6)	14 (11)	13 (9)	.. 96.3
IV	20 (9)	23 (8)	..	.. 87.0	20 (9)	22 (7)	20 (8)	.. 95.2
			..	..				..

The percentages of the season's growth completed before capture varied considerably in the age groups of each year's collection (Tables 46, 47, and 48). Some of the variations, without doubt, are traceable to the small numbers of specimens³⁸ in certain age groups. Because of the selection of the larger II-group fish by the nets (p. 197) it is possible that the estimated percentage of the season's growth completed by this age group is slightly too high. Other variations appear to represent real differences in the course of the season's growth, correlated with sex and age.

At the time of capture the males had, on the whole, completed a lesser percentage of the total season's growth than the females. In the 11 age groups (all three years) for which data were available for both sexes the average percentages were 74.8 for the males and 81.4 for the females. It follows then that the growth of the males exceeds that of the females in the latter part of the season.

An analysis of the actual growth increments (Table 49) reveals that the greater late-season growth of the males accounts in large measure for the superior growth rate of that sex. At capture, 11 age groups of males had completed 15.36 millimeters of the average total of 19.68 millimeters of growth they would have been expected to make had they survived to the end of the season. The corresponding average "partial" growth of females was 14.82 millimeters as compared with an average total growth of 17.41 millimeters. The advantage of the males' growth for the current seasons was 0.54 millimeter at the time of the collections, but the full-season advantage was 2.27 millimeters. In other words, at the time of collection the males had established less than one-fourth of the full-season advantage over the females although they had completed approximately three-fourths of the season's growth. The remaining three-fourths (1.73 millimeters) of the advantage of the males was established in late season during a period in which the males completed only a quarter of the season's growth.

³⁸ With the exception of the 1935 III-group, the data for all age groups represented by less than five fish were excluded from Tables 46, 47, and 48. Several age groups included in the tables nevertheless contained too few specimens to give highly reliable averages.

TABLE 47. Comparison of the calculated growth in millimeters of eight age groups of Nebish Lake rock bass in 1931 up to the time of capture, July 29 to August 6, with the growth for the entire season as calculated from 1932 and 1935 collections of the same year classes. Numbers of specimens in parentheses.

Age in 1931	Males			Females		
	1931 growth up to time of capture	Total 1931 growth computed from collection	Percentage of year's growth completed at capture	1931 growth up to time of capture	Total 1931 growth computed from collection	Percentage of year's growth completed at capture
X	..	..	..	6 (17)	8 (13)	75.0
IX	.. 4 (18)	.. 7 (10)	.. 57.1	5 (47)	7 (33)	.. 71.4
VIII	5 (117)	8 (41)	.. 62.5	5 (99)	8 (74)	.. 62.5
VII	5 (27)	7 (8)	.. 71.4	6 (24)	7 (17)	.. 86.7
VI	10 (5)	16 (5)	.. 62.5	9 (11)	12 (9)	.. 75.0
V	..	..	..	19 (7)	20 (8)	.. 95.0
III	.. 24 (6)	.. 33 (7)	.. 72.7	25 (7)	30 (9)	.. 83.3
II	26 (10)	34 (43)	.. 76.5	25 (9)	30 (59)	.. 82.0
			..		31 (9)	..

TABLE 48. *Comparison of the calculated growth in millimeters of two age groups of Nebish Lake rock bass in 1932 up to the time of capture, August 6 to 11, with the growth for the entire season as calculated from 1935 collections of the same year classes. Numbers of specimens in parentheses.*

Age in 1932	Males			Females		
	1932 growth up to time of capture	Total 1932 growth computed from 1935 collection	Percentage of year's growth completed at capture	1932 growth up to time of capture	Total 1932 growth computed from 1935 collection	Percentage of year's growth completed at capture
III	26 (43)	33 (4)	78.8 ..	25 (59)	27 (9)	92.6 ..
II	28 (78)	30 (28)	93.2 ..	26 (59)	29 (43)	89.7 ..

¹ The inclusion of two fish taken on July 12 has no effect on the determination of the average increment.

Two ready explanations of the observed difference in the growth of the sexes suggest themselves. Male rock bass may continue to grow later in the season than do females. It is readily conceivable also that the growth of both sexes may end at approximately the same date but that the males maintain the higher rate of growth through the latter part of the season. Possibly both factors contribute to the sex difference in growth. The slight advantage of the males at capture may depend on more rapid growth or an earlier beginning of the growing season.

The above explanations are concerned with the manner in which sex differences in growth are established rather than with the underlying causes. Hubbs and Cooper (1935) pointed out that a more rapid growth of the males appears to be characteristic of the centrarchids. This relationship is contrary to the usual one in which, "The growth of the sexes is either very similar, or . . . the females grow faster than the males." Hubbs and

TABLE 49. *Comparison of the average growth in millimeters of male and female rock bass of 11 age groups up to the time of capture with the late-season and full-season growth as determined from collections of the same year classes in later years.*

Item	Growth up to time of capture	Growth in entire season	Growth in late season
Growth of males	15.36	19.68	4.32
Growth of females	14.82	17.41	2.59
Advantage of males	0.54	2.27	1.73

Cooper were inclined toward an explanation on the grounds, "that the increased growth of the males has been of selectional significance, enabling them the better to ward off enemies from the nests which they guard so pugnaciously". They found support for their explanation in the fact that among cyprinids males grow more rapidly than females only in those species with nest-building habits.

An earlier seasonal development of the gonads (preliminary to the next year's spawning) in female rock bass with a resultant earlier retardation of growth might well provide the physiological mechanism for the marked difference in the late-season growth of the sexes.

Age as well as sex affects the progress of the season's growth. Comparisons of average percentages for rock bass of the same sex and captured in the same year demonstrate that in 1930 and 1931 rock bass of age-groups V and younger had completed from 11.2 to 28.6 per cent more of the season's growth at capture than had fish of age-groups VI and older (Table 50). (There is some indication that the excess percentage of growth completed by the younger females may have been greater than that of males.) The difference between the older³⁹ and younger rock bass is a matter of age rather than maturity or immaturity, since the IV- and V-group fish, almost all of which were mature (p. 317), shared the high percentages of the still younger age groups.

Although confirmatory evidence from Nebish Lake collections is lacking, it is believed that the relatively advanced growth of the younger rock bass at capture depends on an earlier be-

TABLE 50. *Comparison of the average percentage of the season's growth completed by old and young rock bass at the time of capture in 1930 and 1931. In parentheses, the number of age groups on which each average percentage was based.*

Sex	Item	Year of capture	
		1930	1931
Male	Percentage of growth completed by VI-group and older	75.0(1)	63.4(4)
	Percentage of growth completed by V-group and younger	86.4(2)	74.6(2)
	Excess percentage of younger fish	11.4	11.2
Female	Percentage of growth completed by VI-group and older	67.2(3)	73.9(5)
	Percentage of growth completed by V-group and younger	95.8(2)	86.8(3)
	Excess percentage of younger fish	28.6	13.9

³⁹ The division between older and younger fish is purely arbitrary and was based on the examination of the data of Tables 46 and 47.

ginning of the season's growth. The only information as to the time at which the growth of the Nebish Lake rock bass begins was obtained from a collection of large fish taken by hook and line on July 5 and 6, 1930. Several of these older fish apparently had not yet formed the 1930 annuli on their scales (p. 205). Whether the scales of younger fish taken on the same dates would have exhibited the 1930 annuli is not known. However, direct evidence on the relation between age and the time at which the season's growth begins was obtained from the examination of scales of rock bass taken in Muskellunge Lake, July 1 and 2, 1932. In all of the scales with three or four annuli, the last-formed annulus lay near the edge of the scale. Some of the scales with five clearly defined annuli had a narrow margin of new growth whereas others had a broad margin with an annulus apparently in the process of formation at the extreme edge of the scale. These latter scales were doubtless from VI-group rock bass. Among the older fish the marginal growth of the scale was usually broad; only exceptionally was an annulus forming at the edge. These observations indicate that in Muskellunge Lake the rock bass of age-groups III, IV, and V had grown sufficiently to exhibit clear-cut annuli at a date when annulus formation was still incomplete in fish of greater age. The situation in the Nebish Lake rock bass probably is similar.

GROWTH COMPENSATION

Growth compensation—the tendency for individuals with relatively slow growth in early life to have relatively rapid growth in later years—has been observed in so many species of fish that its occurrence can well be considered general.⁴⁰ Ordinarily growth compensation sets in immediately after the first year of life; that is, the large yearling fish grow more slowly in the second and later years of life than do the small yearlings. The resultant progressive decrease in the difference in length that existed between large and small yearlings may continue at least to the end of the seventh year of life (Van Oosten, 1937).

⁴⁰ The literature on growth compensation is probably too well known to warrant a review of the subject in this paper. Van Oosten (1929) cited numerous examples of growth compensation.

However, the large yearlings usually will retain a part of their original size advantage, even late in life.

The analysis by Hubbs and Cooper (1935) of the relationship between first-year and second-year growth of three species of sunfish (long-eared sunfish, common sunfish, and bluegill) and one hybrid form (common sunfish $\times$ bluegill) failed to reveal the presence of growth compensation in any of these fish. On the contrary, the data for 12 of 13 collections investigated gave positive correlations (usually highly significant) between first-year and second-year growth. The single exception, a group of female long-eared sunfish from Tomahawk Lake, Montmorency County, Michigan, had a coefficient of correlation of -0.42 ± 0.16 between first-year and second-year growth. The number of fish in this collection was only 12, and the coefficient of correlation is of doubtful significance. Hubbs and Cooper had no reliable data for the study of the relationship between first-year growth and growth beyond the second year of life.

The Nebish Lake rock bass collections, with their abundance of old fish, provide an excellent opportunity not only to determine whether the relationship observed by Hubbs and Cooper holds for yet another centrarchid species, but also to examine the relationship between growth in a centrarchid fish in different years of life over a considerably greater number of years. Tabulations of the growth histories of different yearling length-groups have been made for age-groups II and III of the 1932 collections and for the 1923 year class,⁴¹ (1931 VIII-group and 1932 IX-group combined). In all tabulations the sexes were treated separately.

The original (first-year difference) of 9 millimeters between the largest (above 35 millimeters) and smallest (below 31 millimeters) yearling groups of the II-group males of the 1932 collection (Table 51) continued without change to the end of the second year of life and into the third summer up to the time of capture, since both groups had identical growth increments after

⁴¹ Age-group VII of the 1930 collection also was a member of the 1923 year class. However, the growth of this age group disagreed slightly with the growth of fish of the same year class in later collections (Tables 14 and 15). In order to have as completely representative and homogeneous material as possible, age-group VII was excluded from the growth-compensation data for the 1923 year class.

the first year. The differences among all three groups at capture were exactly the same as those that had existed at the end of the first year of life. In the second year of life the medium-sized (31 to 35 millimeters) yearlings lost 1 millimeter of their original 4-millimeter advantage over the small yearlings, but this loss was regained before capture in the third summer.

TABLE 51. *Relationship between length at the end of the first year of life and the growth in length in later years as determined from age-group II of the 1932 collection of Nebish Lake rock bass.*

Sex	Number of fish	Interval of calculated length in millimeters at end of first year	Calculated length at end of year of life			Calculated increment of length in year of life		
			1	2	¹ 3	1	2	¹ 3
Male	18	Less than 31	29	61	88	29	32	27
	33	31 to 35	33	64	92	33	31	28
	27	More than 35	38	70	97	38	32	27
	Maximum difference		9	9	9	..	..	..
Female	17	Less than 31	29	62	87	29	33	25
	27	31 to 35	33	64	89	33	31	25
	15	More than 35	37	69	96	37	32	27
	Maximum difference		8	7	9	..	..	..

¹ Incomplete growing season.

The data for the II-group females differ slightly from those for the males. The original difference of 8 millimeters between the small and large yearlings was reduced to 7 at the end of the second year. However, this 1-millimeter loss was more than made up in the third summer (difference of 9 millimeters at capture). At capture the medium-sized yearlings had lost 2 millimeters of their original 4-millimeter advantage over the small yearlings but the large yearlings had added 3 millimeters to their original 4-millimeter advantage over the medium-sized group.

The most valid conclusion to be drawn from the data for the II-group appears to be that individual differences in length in existence at the end of the first year of life tended to be maintained with little or no change up to the time of capture late in the third summer. This conclusion is in agreement with Hubbs' and Cooper's observation that second-year growth does not compensate differences in length at the end of the first year. It disagrees with their observation that differences in length at the end of the first year are accentuated by the second-year growth.

The large yearlings of both the males and females of the

III-group rock bass of the 1932 collection (Table 52) were able to add to their first-year advantage in length over the small yearlings, but in both sexes a period of compensatory growth followed. In the males the first-year advantage of the large over the small fish (6 millimeters) was unchanged at the end of the second year of life. The third year saw the difference increased to 9 millimeters, but compensatory growth during the fourth summer, prior to capture, reduced the advantage of the large over the small fish to the original 6 millimeters. In the females the increase in the original difference in length (8 millimeters) between the large and small fish occurred in the second rather than in the third year of life. (This change agrees with that described by Hubbs and Cooper.) Growth compensation reduced the difference from 10 millimeters at the end of the second year of life to 6 millimeters (2 millimeters below the original) at the end of the third year and to 4 millimeters at capture in the fourth summer.

TABLE 52. *Relationship between length at the end of the first year of life and the growth in length in later years as determined from age-group III of the 1932 collection of Nebish Lake rock bass.*

Sex	Number of fish	Interval of calculated length in millimeters at end of first year	Calculated length at end of year of life				Calculated increment of length in year of life			
			1	2	3	¹ 4	1	2	3	¹ 4
Male	13	Less than 28	26	58	89	117	26	32	31	28
	15	28 to 30	29	60	96	123	29	31	36	27
	15	More than 30	32	64	98	123	32	32	34	25
	Maximum	difference	6	6	9	6	..	..	..	..
Female	19	Less than 28	26	54	85	111	26	28	31	26
	22	28 to 30	29	59	89	115	29	30	30	26
	18	More than 30	34	64	91	115	34	30	27	24
	Maximum	difference	8	10	6	4	..	..	..	..

¹ Incomplete growing season.

A more complete picture of the relationships among the growth increments of fish of different lengths in various years of life may be had from data based on collections of the 1923 year class (Tables 53 and 54). By means of a combination of the 1931 and 1932 collections of this year class⁴² it was possible to obtain a reliable history of the growth of different sized year-

⁴² The calculated lengths for the ninth year of life were the addition of average annual increments of growth.

lings up to the time of capture late in the tenth growing season.

The three length groups of yearling males of the 1923 year class were separated by successive differences of 5 millimeters (Table 53). The second-year growth in length of the three groups was in the order of their first-year length. The small yearlings (32 millimeters average length) grew 24 millimeters in the second year; the medium-sized yearlings (37 millimeters average length) grew 26 millimeters; and the large first-year fish (42 millimeters average length) had a 27-millimeter growth. The difference between the second-year growth of the large and small yearlings increased the difference in their average size from 10 to 13 millimeters. During the third year the large and small fish had the same increase in length (30 millimeters), and the second-year difference was maintained exactly. The data for the next three years are irregular. The difference in the average length between the extreme yearling size groups dropped to the original 10 millimeters at the end of the fourth year, rose to 12 at the end of the fifth, and was again at the original level at the end of the sixth year. In the later years of life there was a period of clear-cut compensatory growth that began in the sixth year of life and extended to the end of the eighth year. Growth compensation in this period reduced the difference in the average lengths of the large and small fish from 12 to 4 millimeters. The latter difference was maintained through the ninth year and into the tenth up to the time of capture.

TABLE 53. *Relationship between length at the end of the first year of life and the growth in length in later years as determined from the males of the 1923 year class of the Nebish Lake rock bass, 1931 and 1932 collections combined.*

Number of fish	Interval of calculated length in millimeters at end of first year	Calculated length at end of year of life									
		1	2	3	4	5	6	7	8	9	¹ 10
40	Less than 35	32	56	86	114	133	147	160	170	178	182
70	35 to 39	37	63	94	121	140	153	164	172	180	183
48	More than 39	42	69	99	124	145	157	166	174	182	186
Maximum difference		10	13	13	10	12	10	6	4	4	4
Number of fish	Interval of calculated length in millimeters at end of first year	Calculated increment of length in year of life									
		1	2	3	4	5	6	7	8	9	¹ 10
40	Less than 35	32	24	30	28	19	14	13	10	8	4
70	35 to 39	37	26	31	27	19	13	11	8	8	3
48	More than 39	42	27	30	25	21	12	9	8	8	4

¹ Incomplete growing season

The large yearling females of the 1923 year class (Table 54) increased their initial 10-millimeter advantage over small yearling females by 6 millimeters in the second year of life, and added yet another millimeter in the third. There followed a period of compensatory growth (fourth to eighth year of life) which was broken only by an irregularity in the sixth year. (Note a similar irregularity in the fifth year in the data for the males.) Although the growth compensation brought about a material reduction from the largest maximum difference of 17 millimeters, the smallest maximum difference of 8 millimeters was only 2 below the original 10 millimeters.

TABLE 54. *Relationship between length at the end of the first year of life and the growth in length in later years as determined from the females of the 1923 year class of the Nebish Lake rock bass, 1931 and 1932 collections combined.*

Number of fish	Interval of calculated length in millimeters at end of first year	Calculated length at end of year of life									
		1	2	3	4	5	6	7	8	9	¹ 10
57	Less than 35	32	56	83	108	125	136	146	154	162	167
85	35 to 39	37	64	96	114	132	142	151	157	164	168
31	More than 39	42	72	100	121	137	149	155	162	171	175
Maximum difference		10	16	17	13	12	13	9	8	9	8
Number of fish	Interval of calculated length in millimeters at end of first year	Calculated increment of length in year of life									
		1	2	3	4	5	6	7	8	9	¹ 10
57	Less than 35	32	24	27	25	17	11	10	8	8	5
85	35 to 39	37	27	32	18	18	10	9	6	7	4
31	More than 39	42	30	28	21	16	12	6	7	9	4

¹ Incomplete growing season.

A comparison of the data for the males and females of the 1923 year class reveals that growth compensation produced the same reduction (9 millimeters) from the greatest maximum difference between large and small yearlings in each sex. In the males the advantage of the large over the small fish dropped from 13 at the end of the third year to 4 at the end of the eighth. The corresponding reduction in the females was from 17 at the end of the third year to 8 at the end of the eighth. The relatively large differences in length that separated the large and small female yearlings in later years are traceable therefore, not to the absence of compensatory growth, but rather to the excessive advantage of the large fish at the end of the third year of life.

If the data just described for age-groups II and III of the 1932 collection and for the 1923 year class can be considered to

be descriptive of the relationship between first-year size of rock bass and subsequent growth, the presence of considerable variation in the relationship must be recognized. Some of the variations can be brought out by the following brief summary. The original difference in length between large and small yearlings of the II-group males persisted at the end of the second year and late in the third summer. The females of the same age group underwent slight growth compensation in the second year, but the advantage of the large yearlings was increased during the third summer. The first-year difference in length between large and small yearling males of the III-group underwent no change in the second year, but in the third year the large fish increased their advantage by 3 millimeters only to lose the increase through compensatory growth during the fourth summer. In the III-group females there was an immediate increase (in the second year) over the first-year advantage of large fish over small ones, followed by rather pronounced compensatory growth. The males and females of the 1923 year class differed chiefly in the actual extent of the second- and third-year increase with respect to the original advantage of large over small yearlings. This increase was so much greater in the females that subsequent growth compensation, equal to that found in the males, failed to reduce the difference in length between the large and small female rock bass substantially below the first-year level.

In spite of the variations that do occur, it can be stated definitely that the relationship between first-year length and subsequent growth in length in the rock bass differs from that ordinarily found in that compensatory growth does not set in immediately after the first year. First-year advantage in size may be retained over one or two additional years, but more probably it will be increased in the second and/or third year (*cf.* Hubbs and Cooper, 1935). In the later years growth compensation does occur, but this compensatory growth may do little more than bring the difference in length between large and small yearlings back to the first-year level (1923 year-class females). Again, the growth compensation may bring about a substantial reduction in later years of the original differences in length between large and small yearlings (1923 year-class males; 1932 III-group females).

The question now arises as to the explanation for the deviation of the growth of the rock bass from the more common relationship between first-year length and later growth. Hubbs and Cooper (1935) offered four possible explanations for the positive correlation between first-year and second-year growth in three species of sunfish and one hybrid: (1) A "competitive advantage" during the second year traceable to the attainment of large size in the first; (2) the selection and occupancy during both years of a particularly favorable or unfavorable "ecological niche"; (3) some physiological effect of the rate of growth in the first year on rate of growth in the second; (4) "genetic differences in growth potential between different individuals." Conceivably any one of the above causes or any combination of them may contribute to the relationship described for the rock bass. There is no direct evidence available on the question. Nevertheless, there is good reason to believe that a fifth possible contributing factor should be considered in the explanation of the observed relationship in the rock bass between first-year length and later growth. This fifth possible explanation holds that the early increase in or maintenance of the first-year advantage in length and the later "compensatory" growth are to a certain extent "apparent" phenomena having their origin in the comparison of fish of different age (hatched at different times in the season).

The concept that an "apparent" growth compensation may result from the comparison of fish with identical growth curves but of different age is by no means new. Hodgson (1929) demonstrated conclusively that the comparison of annual increments of growth from curves that were *identical* in form but which started at different points on the time axis gave clear-cut examples of growth compensation.⁴³ However, Hodgson was dealing with a form (marine herring) whose annual growth increments decreased continuously, and not with one whose growth curve characteristically contains an inflection.⁴⁴ Consequently,

⁴³ Ford (1933) reviewed Hodgson's observations and added more detailed consideration of certain theoretical aspects of growth compensation.

⁴⁴ The statement that the growth curve of the rock bass characteristically contains an inflection is justified in spite of the fact that no inflection occurred in the general growth curve of the females and the inflection in the general growth curve of the males was not pronounced (p. 235). The

he was not confronted with a temporary increase in the original advantage of large yearlings.

The manner in which differences in age (time of hatching in the season) may affect the comparison of the growth increments of fish whose growth curves contain inflections may be seen from the examination of Figure 13. The curves *a* and *b* which may be taken as typical of large and small yearlings, respectively, are identical in form but originate at different points on the time axis (at t_a and t_b). Because of this difference in age the fish represented by the curve *b* were smaller than those represented by the curve *a* at t_1 , the time of the formation of the first annulus (that is, $AB < AC$); furthermore, the fish of group *b* had the

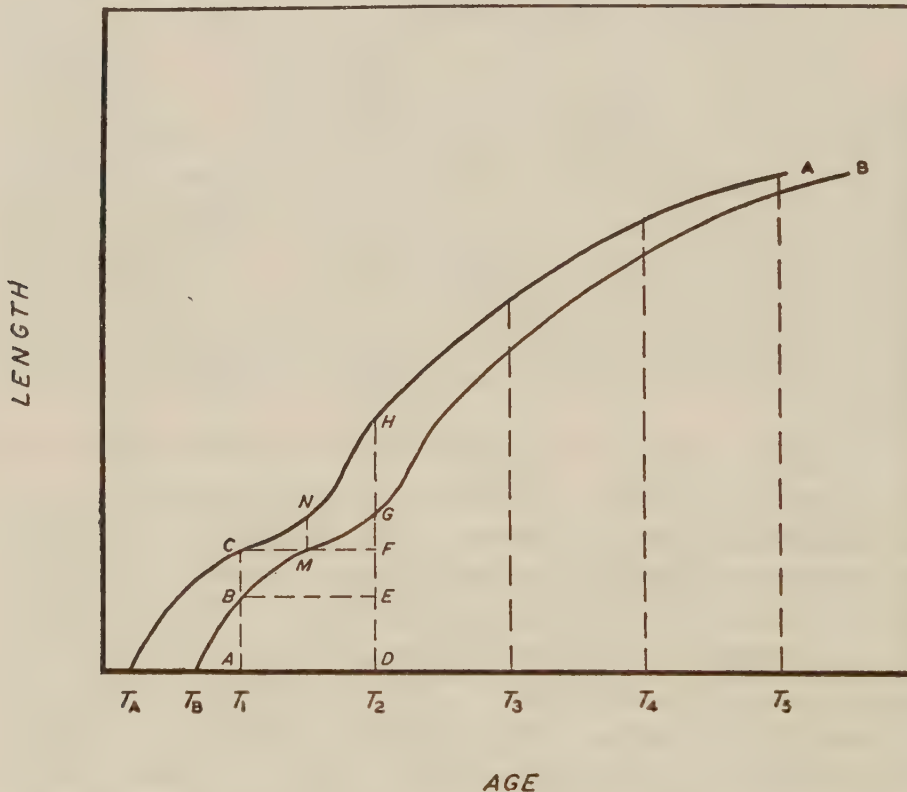


FIGURE 13. Diagram to illustrate the effects of differences in age (time of hatching in the growing season) on the determination of the relationship between the length at the end of the first year of life and growth in later years. See text for explanation.

growth curves for individual fish contain inflections that are obscured in the computation of grand averages since the year of life in which these inflections occur varies from one individual to another. Curves for the year classes may or may not have inflections (Tables 17 and 18, Figs. 5 and 6).

smaller growth increment in the second as well as the first year of life ($GE < FH$). In the later years of life, however, the growth increments of the fish of group *b* exceeded those of the fish of group *a* and growth compensation occurred.

The curves as presented in Figure 13 describe only one particular situation. Only slight modifications of them would be necessary to produce variations similar to those appearing in Tables 51, 52, 53, and 54. As an illustration assume that the second annulus was formed at a point where the difference in length between the fish of groups *a* and *b* = NM, that the first annulus was formed at t_1 and the third at t_2 . In this situation $CB > NM < HG$, and the data would show growth compensation in the second year followed by an increase in the advantage of group *a* in the third (*cf.* II-group females of the 1932 collection, Table 51). Nor would it be difficult to arrange a situation where $CB = NM = HG$, so that the fish of group *a* would retain a constant advantage over 3 years.

It seems, then, that the relationship between first-year length and later growth in length as observed in the rock bass can be duplicated by the comparisons of individuals with the same (theoretical) growth curves but of different age (hatched at different times in the first growing season). It does not appear unreasonable therefore to hold that the average differences in the growth of small, medium-sized, and large yearling size-groups may depend to an important degree on differences in age.

In spite of the evidence that the observed relationships among the annual growth increments may depend in part on differences in age, it would not be valid to contend that age differences alone are responsible. The explanations offered by Hubbs and Cooper for the positive correlation between first-year and second-year growth in sunfishes are biologically sound and therefore must be given consideration along with any other possible explanation. Furthermore, the thesis that growth compensation as a true rather than an apparent phenomenon does not occur among fishes is untenable in the face of known facts. For example, the well-known fact that salmon with an extended stream life grow more rapidly in the sea than do fish that are in the same year of life but which spent a lesser number of years in the stream can not well be interpreted as other than true growth compensation.

A wealth of experimental evidence supports the view that

among animals in general the inherent capacity for growth is lost chiefly through its exercise, and, conversely, the failure to grow does not entail necessarily the loss of the natural ability to grow. Experiments that involved the complete suppression of growth of the albino rat over periods of more than 408 days led Osborne and Mendel (1915) to conclude that, "The growth impulse or capacity to grow, can be retained and exercised at periods far beyond the age at which growth ordinarily ceases." From similar experiments with the albino mouse Thompson and Mendel (1918)⁴⁵ made the following observations on the growth of mice following long periods of growth suppression: "While a few cases of permanent stunting have been observed, the rate of growth, instead of being decreased, proves to be accelerated after suppression."

Observations to the effect that the ability to grow is maintained over long periods of inhibited growth are by no means limited to experiments with mammals. Similar results have been obtained for such widely separated groups as fish (Titcomb *et al.*, 1928), salamanders (Springer, 1909; Morgulis, 1912), and insects (Zabinski, 1929). Of specific application to the problem of growth compensation in fish is the observation of Titcomb *et al.*, that brook trout (*Salvelinus fontinalis*) subjected to continuous stunting for as long as 7 months not only retain the capacity for growth at the optimum rate but, "in some cases show an increased rate above our optimum."

The existence of growth compensation in fish as a true rather than "apparent" phenomenon must be recognized. However, the precise extent to which compensatory growth takes place may be obscured through the simultaneous occurrence of an "apparent" growth compensation traceable to differences in age (time of hatching in the season).

LENGTH-WEIGHT RELATIONSHIP AND CONDITION ANNUAL AND SEASONAL FLUCTUATIONS IN THE LENGTH-WEIGHT RELATIONSHIP

Tabulations of the length-weight relationship of the Nebish Lake rock bass were prepared for each collection,⁴⁶ sexes sep-

⁴⁵ This publication contains numerous references to the literature on the effects of the suppression of growth on later growth on adequate diets.

⁴⁶ The July and August samples of 1930 were treated as separate collections.

arately. The examination of the data failed to reveal any consistent differences among the August, 1930, the 1931, and the 1932 materials. Consequently, these three collections were combined to form a general length-weight table (Table 55). The length-weight relationships as determined for the fish taken in July, 1930, and in 1935 are to be found in Table 56.

In Table 55, whose data may be considered descriptive of the length-weight relationship of the rock bass in late July and early August,⁴⁷ tabulations have been made for males and females separately and for the sexes combined. There is detectable a tendency for female rock bass to be slightly heavier than males of the same length. However, the differences are not large; neither are they consistent in their occurrence. A combination of the data for the sexes is therefore justifiable. This combination (at the right of the table) includes the small 1930 and 1931 specimens for which there were no sex records. There has been added also a tabulation of total length in inches⁴⁸ and weight in ounces. This general relationship is presented graphically in Figure 14.

It may be seen that the weight of the Nebish Lake rock bass at the minimum legal length of 7 inches is 3.3 ounces. Certainly, the present length limit imposes no hardship on anglers, for few would care to keep fish of less weight. The approximate total lengths at which weights of 4, 6, and 8 ounces are attained are 7.5, 8.5, and 9.5 inches, respectively. Only the largest males (average length, 9.6 inches) had an average weight in excess of a half pound.

The rock bass taken in July, 1930, were lighter, and those captured in August, 1935, were heavier (Table 56) than fish of corresponding lengths collected in August, 1930, and in 1931 and 1932. Since the rock bass of the July, 1930, collection were lighter than fish taken in August of the same year, their relatively low weights may be considered the result of the time of capture in the growing season. The rock bass captured in July,

⁴⁷ For dates of collection in each year see Table 2.

⁴⁸ Since female rock bass have a relatively shorter tail than males at lengths of 160 millimeters and greater (Table 11) the factor employed for the conversion of standard to total length over the interval, 162 to 191 millimeters, was 0.0477, the mean of the factors for the sexes. At the lengths 196 and 200 millimeters, which were represented by males only, the factor, 0.0479 was used.

TABLE 55. *Length-weight relationship of the Nebish Lake rock bass as determined from the combination of the August, 1930, collection and the complete collections of 1931 and 1932.*

Males			Females			Sexes combined		
Number of fish	S. L. ¹ in millimeters	Weight in grams	Number of fish	S. L. in millimeters	Weight in grams	Number of fish	S. L. in millimeters	Weight in grams
3	200	251	..	...	...	3	200	251
3	196	218	..	...	...	3	196	218
13	191	199	..	191	203	18	191	200
44	186	185	4	187	191	48	186	185
70	182	173	22	181	173	92	182	173
62	177	163	62	177	161	124	177	162
62	172	154	84	172	152	146	172	153
14	166	138	61	167	140	75	167	140
12	162	125	74	162	125	86	162	125
12	156	112	57	157	113	62	157	113
5	152	104	54	152	105	66	152	105
12	147	93	28	147	94	37	147	94
9	143	81	19	143	86	32	143	84
13	137	73	9	138	79	15	138	77
6	132	65	8	131	66	16	132	66
8	127	58	6	127	61	14	127	59
23	121	52	17	121	50	41	121	51
10	118	48	28	117	46	43	117	47
7	112	40	17	112	40	26	112	40
6	106	32	8	107	35	16	107	34
14	102	30	12	103	31	27	102	30
11	96	25	6	96	26	20	96	25
25	91	21	25	91	21	56	91	21
30	87	19	25	87	19	74	87	19
5	82	16	8	83	18	38	82	17
..	...	..	..	..	..	13	78	14
1	74	12	..	..	..	3	72	12

¹S. L. = standard length; T. L. = total length

²Actual value = 0.741.

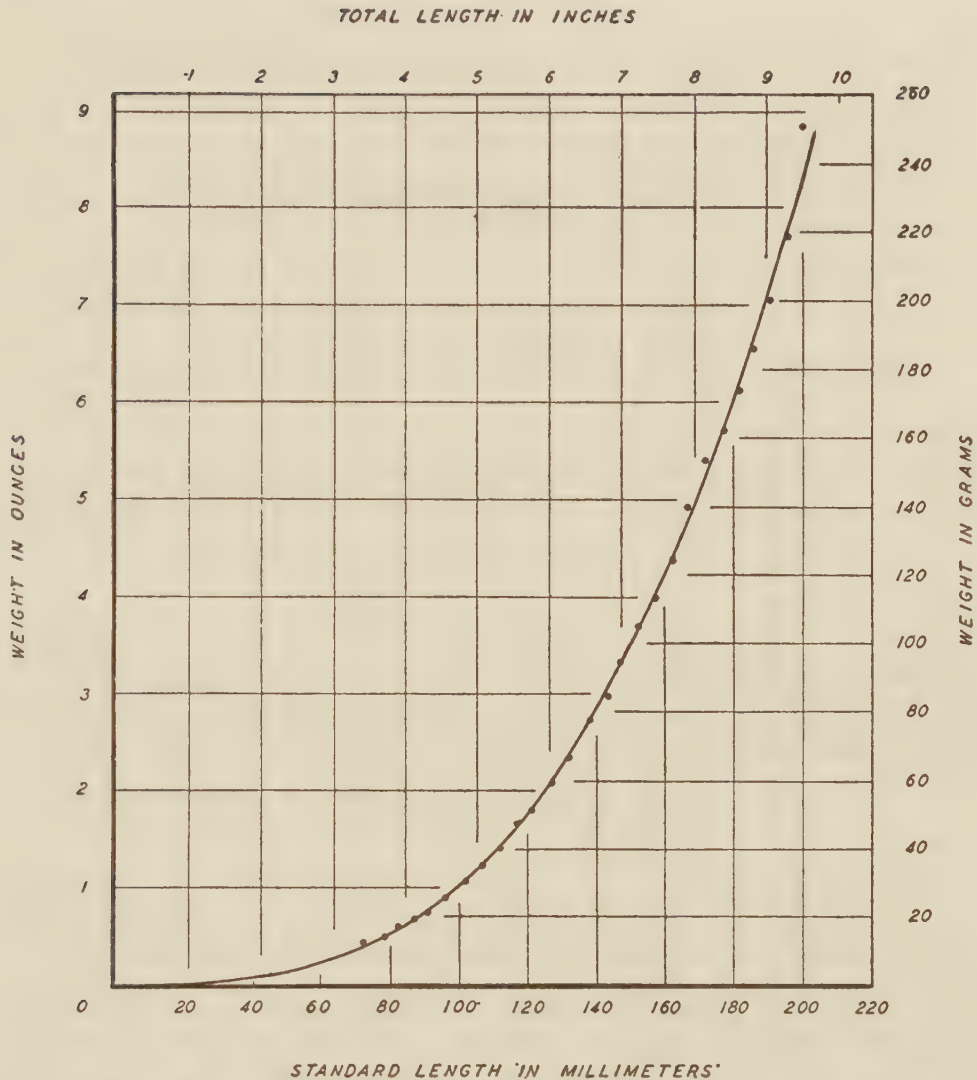


FIGURE 14. Length-weight relationship of the Nebish Lake rock bass (sexes combined) as determined from the combined collections of August 1930, and late July and early August 1931 and 1932. The curve is the graph of the equation fitted to the length-weight data, and the dots represent the empirical averages of length and weight.

1930, differed further from other rock bass taken in the years, 1930 to 1932, in the tendency for females to be lighter, not heavier, than males of the same length.

The time of capture in the growing season possibly may account for the relatively high weights of the rock bass of the 1935 sample. It was pointed out in the preceding paragraph that in 1930 rock bass became relatively heavier between early

TABLE 56. *Length-weight relationship of the Nebish Lake rock bass of the collections of July 5 and 6, 1930, and August 28, 1935. There were no sex differences in the 1935 collection.*

July, 1930					1935			
Males			Females		Sexes combined			
Number of fish	S. L. ¹ in millimeters	Weight in grams	Number of fish	S. L. in millimeters	Weight in grams	Number of fish	S. L. in millimeters	Weight in grams
2	180	150	..	..	..	..	..	..
11	176	148	3	179	147	1	177	177
24	172	134	6	171	124	3	172	177
22	167	128	2	166	116	1	166	146
18	162	120	17	162	113	4	161	154
10	157	111	17	157	110	10	157	131
1	153	102	12	152	101	16	152	122
1	147	98	1	145	92	17	146	108
..	..	..	3	143	80	16	141	98
1	136	68	1	135	64	14	137	89
..	..	..	..	..	..	13	132	83
..	..	..	..	..	..	5	127	74
..	..	..	..	..	..	4	123	71
..	..	..	..	..	..	1	111	51

¹ S. L. = standard length.

July and early August. If this trend were to continue, the 1935 fish which were captured later in the season than were the rock bass of any previous year (Table 2) might be expected to be heavier than late-July and early-August fish of 1930 to 1932. However, in the absence of comparative material from earlier dates in the 1935 season, the possibility of an explanation on the grounds of an annual fluctuation in the length-weight relationship must not be overlooked.

MATHEMATICAL RELATIONSHIP BETWEEN LENGTH AND WEIGHT

Authors who have investigated the length-weight relationship of fish frequently have mentioned the fact that if form and specific gravity remain constant, this relationship can be expressed in mathematical terms by the equation:

$$W = CL^3,$$

where

$C =$ a constant.

Although the cubic parabola does describe the length-weight relationship accurately in some species, exceptions appear to be the rule, and in most forms better results are obtained by the use of the general equation:

$$W = CL^n,$$

where

$C =$ a constant,

and

$n =$ a constant.

The fitting of a parabola to the length-weight data of Table 55 (sexes combined) revealed that for those collections of the Nebish Lake rock bass the length-weight relationship follows the "cube law" almost exactly. The empirical equation was determined as:

$$W = 2.884 \times 10^{-5} L^{3.003},$$

where

$W =$ weight in grams,

and

$L =$ length in millimeters.

In logarithmic form the equation may be stated:

$$\log W = -4.54002175 + 3.003 \log L.$$

The comparison of the actual and the theoretical or calculated weights (Table 57) shows that the above equation fits the empirical data reasonably well. The 17-gram discrepancy at an average length of 200 millimeters (only three fish—see Table 55) provides the only large deviation of the calculated from the actual weight. Other deviations of as much as 4 grams occur

TABLE 57. *Comparison of actual and calculated weights of rock bass taken in August, 1930, and in 1931 and 1932, sexes combined.*

Standard length in millimeters	Actual weight in grams	Calculated weight in grams	Standard length in millimeters	Actual weight in grams	Calculated weight in grams	Standard length in millimeters	Actual weight in grams	Calculated weight in grams
200	251	234	157	113	113	112	40	41
196	218	221	152	105	103	107	34	36
191	200	204	147	94	93	102	30	31
186	185	189	143	84	86	96	25	26
182	173	177	138	77	77	91	21	22
177	162	162	132	66	67	87	19	19
172	153	149	127	59	60	82	17	16
167	140	136	121	51	52	78	14	14
162	125	124	117	47	47	72	12	11

among the larger fish, but below the length of 167 millimeters the maximum deviation is 2 grams. For all length groups the mean of the absolute values of the deviations is only a little more than 2 grams.

CONDITION

Further information on the length-weight relationship of the rock bass may be obtained through the study of the coefficient of condition, K , whose value is calculated from the equation:

$$K = \frac{W \times 10^5}{L^3},$$

where

W = weight in grams,

and

L = length in millimeters.

The chief value of the coefficient of condition lies in the fact that K is a direct measure of plumpness or relative heaviness. Values of K can be compared, therefore, between fish of any size. The coefficient of condition was calculated for every Nebish Lake rock bass whose age was determined.

Table 58 contains a record of the average value of the coefficient of each age group (sexes separately) in each year's collection. The data for the three years, 1930 to 1932, resemble each other rather closely. There are differences, it is true, between the averages of K for fish of the same age taken in different years, but these discrepancies are in general not large and are random in their distribution. Females tend to have slightly higher values of K than males of the same age. The large values of K of the rock bass of the 1935 collection reflect a situation described previously (p. 307).

The changes of condition that accompany increase in age may be described from the averages of K for different age groups based on a combination of the 1930-1932 material. The variations of K with increase in age are decidedly irregular, but fish of both sexes nevertheless exhibit a tendency to become more plump as they grow older. This tendency is brought out much more clearly by the following tabulation based on combinations of age groups (number of specimens in parentheses):

TABLE 58. Coefficient of condition, K, according to sex, age, and year of collection, and K according to age and sex for the 1930, 1931, and 1932 collections combined. Number of specimens in parentheses.

Age group	Males				Average K for 1930, 1931 and 1932	Age group	Females				Average K for 1930, 1931 and 1932
	Year of capture						Year of capture				
	1930 ¹	1931	1932	1935			1930 ¹	1931	1932	1935	
II	...	2.84 (10)	2.79 (78)	...	2.80 (88)	II	...	2.95 (9)	2.83 (59)	...	2.85 (68)
III	...	2.80 (6)	2.87 (43)	...	2.86 (49)	III	...	2.81 (7)	2.88 (59)	3.73 (1)	2.87 (66)
IV	...	2.85 (3)	2.79 (7)	...	2.84 (19)	IV	2.89 (9)	2.95 (5)	2.84 (9)	3.52 (8)	2.88 (23)
V	2.87 (9)	2.97 (8)	2.84 (8)	3.44 (5)	2.91 (25)	V	3.00 (6)	3.01 (7)	2.86 (2)	3.53 (43)	2.99 (15)
VI	2.93 (9)	2.88 (5)	2.89 (3)	3.64 (4)	2.87 (11)	VI	2.94 (6)	2.87 (10)	2.90 (8)	3.44 (9)	2.90 (24)
VII	2.85 (3)	2.92 (27)	2.90 (5)	...	2.92 (47)	VII	2.91 (43)	2.95 (24)	2.95 (9)	...	2.93 (76)
VIII	2.94 (15)	2.95 (117)	2.83 (8)	...	2.94 (128)	VIII	3.02 (8)	2.98 (99)	2.93 (17)	3.54 (1)	2.98 (124)
IX	2.93 (3)	2.98 (18)	2.94 (41)	...	2.95 (61)	IX	3.04 (2)	3.03 (47)	2.96 (74)	...	2.99 (123)
X	3.00 (2)	2.92 (4)	2.93 (10)	3.56 (1)	2.93 (14)	X	2.90 (1)	2.93 (17)	2.97 (33)	...	2.96 (51)
XI	...	...	3.03 (3)	...	3.03 (3)	XI	...	3.04 (2)	3.07 (13)	3.19 (1)	3.07 (15)
XII	...	...	...	...	...	XII	...	3.06 (1)	3.00 (3)	...	3.02 (4)
XIII	...	...	...	...	...	XIII	...	...	3.03 (1)	...	3.03 (1)

¹ August collection only; no age-determinations were made for fish taken in July, 1930.

Age groups	Average <i>K</i>	
	Males	Females
II, III, IV	2.82 (156)	2.86 (157)
V, VI, VII	2.91 (83)	2.93 (115)
VIII, IX, X	2.94 (203)	2.98 (298)
XI, XII, XIII	3.03 (3)	3.06 (20)

Coefficients of condition were calculated for a small collection of rock bass from Lake Wawasee in northern Indiana by Hile (1931). The collections were made in late June and in July, 1926 to 1928. The average *K* of the Wawasee rock bass (the range of ages covered was II to VII) was 3.25. A comparison with the Nebish Lake fish shows that the average *K* of the specimens from Lake Wawasee was intermediate to the averages found for the Nebish Lake stock in 1930 to 1932 and in 1935.

AGE AT MATURITY

All rock bass of age-group V or older were sexually mature.⁴⁹ Data on the maturity of the younger age groups (II, III, and IV), in the different years' collections are presented in Table 59. Differences in the nature of the available information for the different collections should be mentioned. In 1930 and 1931 the immature individuals simply were designated as such without record of sex. For these years it has been possible, therefore, to compute the percentage of maturity for the entire age groups but not for the sexes separately. The complete sex records for the 1932 collection have permitted the determination of the percentage of mature fish of each sex in each age group as well as in the age group as a whole. Records of maturity were not made for those 1932 specimens that were preserved for use in the study of the body-scale relationship. Only mature fish were captured in 1935.

⁴⁹ A fish whose state of organs indicated that it would spawn the next season was designated as mature, even when it was relatively certain that it had not spawned during the year it was captured.

The time of capture within the season (late July and early August) introduced a degree of uncertainty into the determination of the state of maturity of the smaller fish. The collections were made before the autumnal development of the gonads (preliminary to the next year's spawning) had set in, but at a time when the gonads of fish that had spawned in the year of capture had recovered from the post-spawning condition. Any possible distorting effect of errors in the assessment of the stage of maturity has been reduced greatly by the fact that all determinations were made by the same individual—Dr. Edward Schnerberger—and therefore were based on the same criteria.

The youngest age group that contained mature individuals was the II-group. These fish would have spawned the next year at the end of the third full year of life (beginning of the fourth year). It is most unlikely that any of these II-group rock bass had spawned in the year of capture.⁵⁰ The oldest age group that contained immature rock bass was the IV-group. These immature fish would not have spawned at the end of the fifth year of life (beginning of the sixth), but the fact that all V-group rock bass were found to be mature indicates that they would have spawned at the end of the sixth year (beginning of seventh). It may be stated, therefore, that the age of the Nebish Lake rock bass at the first spawning, expressed in completed years of life, varies from 3 to 6.

The sexes reach maturity at approximately the same age. In the 1932 collection 59 per cent of the II-group males and 47 per cent of the II-group females were mature. The difference of 12 per cent cannot be considered important. In age-group III all of the 46 females and all but 2 of the 28 males were mature. Here, again, the difference between the sexes is not significant.

There was a general tendency for the percentage of mature fish at a particular age to increase over the 3-year period, 1930 to 1932. Twenty-five per cent of the 1930 IV-group were immature but all fish of this age group were mature in later years.

⁵⁰ Age-group I was not represented in the 1930-1932 or the 1935 collections. However 10 I-group fish, captured (by means of a small-mesh fyke net) and examined in the summer of 1938 by staff members of the Wisconsin Geological and Natural History Survey, were all immature. The ages of these rock bass, whose lengths ranged from 56 to 76 millimeters, were determined by scale examinations.

The percentages of maturity of age-group III increased from 0 in 1930 to 93 in 1931 and to 97 in 1932. For age-group II the corresponding percentages were 0, 32, and 54.

The average length of an age group appears to be related to the percentage of mature individuals. This relationship is brought out sharply by the summary in Table 60 which permits a ready comparison of the annual fluctuations with respect to the average length of the age groups and with respect to the percentage of mature fish. The 1930 IV-group which was the only IV-group that contained immature individuals also had the lowest average length for fish of that age. In age-groups II and III each increase in average length was accompanied by a rise in the percentage of mature fish. (The single III-group rock bass captured in 1935—Table 59—may be disregarded.) The belief that the average size of an age group influences the percentages of maturity finds support in the observation (Table 59) that mature rock bass were consistently longer than immature fish of the same age and captured in the same year. (The 1931 III-group provides an exception, but this age group contained only one immature fish.) The data for 1932 demonstrate that the length advantage of the mature fish holds for the sexes separately as well as combined.

The data of Table 60 give some evidence that slow growth may in itself delay the attainment of maturity. For example, all individuals of the 1930 III-group were immature whereas the II-groups of 1931 and 1932, despite their smaller size, were 32 and 54 per cent, respectively, mature. Similarly the slowly growing 1930 IV-group contained a higher percentage of immature rock bass than did the slightly shorter III-groups of 1931 and 1932. Maturity appears, then, to depend on both size and

TABLE 60. *Relationship between the average length (in millimeters) and the percentage of mature individuals (sexes combined) in three age groups of the 1930-1932 collections of the Nebish Lake rock bass.*

Age group	Item	Year of capture		
		1930	1931	1932
IV	Average length	121	129	145
	Percentage mature	75	100	100
III	Average length	99	114	118
	Percentage mature	0	93	97
II	Average length	80	86	91
	Percentage mature	0	32	54

age. Within an age group the longer fish are the more likely to be mature, but among fish of similar size, the younger are the more likely to be mature. In other words, rapid growth seems to be correlated with an earlier attainment of maturity.⁵¹

The legal size limit of 7 inches, total length, (146 millimeters, standard length) is fully adequate for the protection of the immature Nebish Lake rock bass. The largest immature specimen in the collections had a length of only 5.9 inches (123 millimeters). In fact, only 11 or 8.5 per cent of 129 immature individuals exceeded a length of 5 inches (104 millimeters).

SEX RATIO

Among the rock bass for which there were sex records the females exceeded the males in abundance in each year's collection (Table 61). Records of sex were complete in 1932 and 1935. The sex was not recorded for the small, immature individuals in 1930 and 1931. In all collections combined there were 135 females per 100 males.

The incomplete records of 1930 and 1931 make the sex ratios of the different collections unreliable for comparisons of the relative abundance of the sexes in the samples taken in different calendar years. A better measure of fluctuations in the sex ratio of the different years' samples can be had from the following ratios computed from fish of age-group IV and older (practically all of the fish for which there were no sex records were members of age-groups II and III):

Year of capture	Number of males	Number of females	Females per 100 males
1930	41	75	183
1931	182	213	117
1932	85	169	199
1935	38	62	163

For rock bass older than the III-group the number of females per 100 males varied from a minimum of 117 in 1931 to a maximum of 199 in 1932. It is doubtful whether even these ratios can be accepted as precise measures of the relative abundance of

⁵¹ This relationship may have its application within a population rather than between different populations. It is well known that so-called "dwarf" stocks of several species may mature at an exceptionally small size.

TABLE 61. *Numerical representation of the sexes in each age group of each year's collection and for each age group with all collections combined. Below, the sex ratio for each age group of the combined collections.*

Year of Capture	Item	Age group											Total	Females per 100 males
		II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	
1930	Number of males	..	..	9	9	3	15	3	2	..	..	..	..	41
	Number of females	..	..	9	6	6	43	8	2	1	..	..	..	75
	Number of males	10	6	3	8	5	27	117	18	4	..	..	..	198
1931	Number of females	9	7	5	7	11	24	99	47	17	2	1	..	229
	Number of males	78	43	7	8	3	5	8	41	10	3	..	..	206
	Number of females	59	59	9	2	8	9	17	74	33	13	3	1	287
1932	Number of males	..	..	5	28	4	..	..	..	1	..	..	..	38
	Number of females	..	1	8	43	9	..	1	..	..	1	..	..	63
	Number of males	88	49	24	53	15	47	128	61	15	3	..	..	483
1930 to 1932 and 1935	Number of females	68	67	31	58	34	76	125	123	51	16	4	1	654
	Females per 100 males	77	137	129	109	227	162	98	202	340	533	..	..	135

the sexes in the adult population. In one year (1931), at least, gear selection appears to have distorted the ratio (p. 322). It is valid nevertheless to state that a predominance of females is characteristic of the mature fish.

The variation of the sex ratio with age was irregular (Table 61). It is apparent, however, that females were strongly predominant at the higher ages (age-group IX and older). In all collections combined the males exceeded the females in number in only 2 (age-groups II and VIII) of the 12 age groups represented.

In spite of the great irregularity in the relationship between the sex ratio and age, the following tabulation wherein the age groups have been combined three at a time does give some indication of a general trend toward a greater relative abundance of females with increase in age:

Age Groups	Number of males	Number of females	Females per 100 males
II, III, IV	161	167	104
V, VI, VII	115	168	146
VIII, IX, X	204	299	147
XI, XII, XIII	3	21	700

In the combined data of all collections age-group VIII was the only one above age-group II in which the males outnumbered the females. If the 1931 VIII-group were excluded, the combined VIII-groups would contain 11 males and 26 females for a ratio of 236 females per 100 males. Furthermore, the exclusion of the 1931 VIII-group from the combined data for age-groups VIII, IX, and X would increase the sex ratio for those age groups from the listed value of 147 to the much higher figure of 230 females per 100 males.

There is good reason to believe that the sex ratios, 236 females per 100 males for age-group VIII and 230 females per 100 males for age-groups VIII to X, are more descriptive of true conditions than the corresponding values of 98 and 147 calculated from material that included the 1931 VIII-group. The high representation of males in that age group is in disagreement not only with the other VIII-group samples but also with

earlier and later samples of the same (1923) year class—the 1930 VII-group and the 1932 IX-group. An even more convincing argument for the exclusion of the 1931 VIII-group from the sex-ratio data is to be had from direct evidence that the exceptional scarcity of females in the samples of that group can be attributed to the selective action of gill nets.

The investigation of the rôle of gill-net selection on the determination of the sex ratio in the 1931 VIII-group may be confined to a study of the action of the 2½-inch and 3-inch mesh nets since nets of these two mesh sizes accounted for 110 of a total of 115 males and 87 of a total of 99 females of that age group taken in gill nets. The reason for the failure of the 2½-inch and 3-inch mesh gill nets to take a greater number of VIII-group females in 1931 can be brought out by a comparison of the length distributions of the VIII-group rock bass, according to sex, with the length distributions of rock bass that can be taken efficiently by nets of the two sizes of mesh (Table 62). Although nets with both 2½-inch and 3-inch meshes took rock bass over a rather large range of length, the limits within which the two sizes of mesh operated on the Nebish Lake stock with reasonably good efficiency may be set at approximately 145 to 184 millimeters and 165 to 194 millimeters respectively. These “limits of efficiency”, which are admittedly arbitrary to a certain extent, have been indicated in Table 62 by horizontal lines.

Differences in the percentages of males and females whose lengths fell within the “limits of efficiency” of the two nets led to differences in the actual fishing intensity to which the sexes were subjected. Eighty-eight per cent of the males were of a length that could be captured by the 2½-inch mesh net and 98 per cent could be taken readily by the 3-inch mesh net (Table 63). All of the females were of a size that could be taken by the 2½-inch mesh net but only 26 per cent were sufficiently long to be taken easily by the 3-inch mesh net. As a result of this situation practically all of the males were subject to capture by either of two nets; the females, on the other hand, were sampled effectively by the 2½-inch mesh net only. The predominance of males in the samples of the 1931 VIII-group may be attributed, therefore, to the greater fishing intensity for fish of that sex.

TABLE 62. Comparison of length distributions of VIII-group rock bass of 1931 and IX-group rock bass of 1932 with the length distributions of the total catch of 2½-inch and 3-inch mesh gill nets, 1931 and 1932 collections combined. The heavy horizontal lines set off the limits of effectiveness of the two meshes of gill net. Fish taken by hook and line have been omitted from the frequencies for the age groups.

Length interval in millimeters	Age group or mesh size					
	1931 VIII-group males	1931 VIII-group females	2½-inch mesh, all ages, 1931-32	3-inch mesh, all ages, 1931-32	1932 IX-group males	1932 IX-group females
200 to 204	..	..	1	1	..	..
195 to 199	1	..	..	3	1	..
190 to 194	..	..	2	13	5	1
185 to 189	13	..	5	40	10	..
180 to 184	34	..	14	69	12	1
175 to 179	28	2	13	100	9	12
170 to 174	30	14	34	85	3	21
165 to 169	8	10	24	30	..	14
160 to 164	..	31	45	5	..	15
155 to 159	..	22	36	2	..	4
150 to 154	1	19	32	..	..	..
145 to 149	..	1	12	1	..	..
140 to 144	..	..	5	..	..	..
135 to 139	..	..	1	..	..	..
Total number	115	99	224	1350	40	68

¹ One fish in interval, 115 to 119 millimeters, not shown in table.

The increase in the length of rock bass of the 1923 year class from 1931 to 1932 was sufficient to reduce greatly the distorting effects of gear selection on the determination of the sex ratio. The data of Tables 62 and 63 for the 1932 IX-group indicate a much more nearly equal fishing intensity for the sexes. In a corresponding manner the sex ratios as determined from the combined samples of the 2½-inch and 3-inch mesh nets and from the samples of all gears (including hook and line) were more nearly in conformity with the results for other samples of the older age groups.

TABLE 63. *Effect of the selective action of gill nets on the determination of the sex ratios of the 1931 VIII-group and the 1932 IX-group of the 1923 year class. See text for definition of "range of efficiency".*

Age group	Sex	Item	Gear			¹ All gears
			2½-inch mesh gill net	3-inch mesh gill net	2½- and 3-inch meshes	
VIII	Male	Number taken by gear	28	82	110	117
		Percentage within range of efficiency	88	98	..	..
	Female	Number taken by gear	64	23	87	99
		Percentage within range of efficiency	100	26	..	..
		Sex ratio (females per 100 males)	229	28	79	85
IX	Male	Number taken by gear	6	29	35	41
		Percentage within range of efficiency	60	98	..	..
	Female	Number taken by gear	27	22	49	74
		Percentage within range of efficiency	99	72	..	..
		Sex ratio (females per 100 males)	450	76	140	180

¹ Includes rock bass taken by hook and line.

Gill-net selectivity doubtless affected the determination of the sex ratio in other individual age groups, but annual differences in the sizes of gill-net mesh employed and in the length distribution of fish at a particular age may have prevented the distortion of the data for the combined samples of any one age group. (For example, 1931 was the only year in which age-group VIII showed a predominance of males.) The distorted sex ratio of the sample of the 1931 VIII-group was exceptionally damaging to the general data on the relationship between the sex ratio and age because of the much smaller numbers of specimens in the VIII-group samples of other years. The effect of a similar predominance of males in 1931 VII-group⁵² was reduced greatly because of the scarcity of males in the 1930 and 1932 samples of the VII-group.

The preceding detailed discussion of the effect of gear selection on the determination of the sex ratio was undertaken primarily to establish the validity of the general conclusion that the relative abundance of females tends to increase with increase in age. The data presented serve further to illustrate the extreme caution that must be observed in the use of gill-net samples for biological studies, and the importance of fishing with a wide variety of mesh sizes. The distortion of the sex-ratio data for the 1931 VIII-group most probably could have been avoided or at least reduced by the use of a $2\frac{3}{4}$ -inch mesh net along with the $2\frac{1}{2}$ -inch and 3-inch meshes.

The increase in the relative abundance of the females with an increase in age points toward a differential mortality of the sexes. This differential mortality conceivably may be the result of a greater destruction of the males in the sports fishery or by predators, or it may depend on sex differences in the natural mortality rate; that is, the females may be inherently more viable than the males.

There are strong arguments against an explanation of the changing sex ratio on the basis of either of the first two of the three suggested possible causes listed above. It is true that the

⁵² Gill-net selectivity probably accounts for the abundance of males in the 1931 VII-group as well as in the VIII-group. The males of the two age groups had the same length, and the VII-group females were only 2 millimeters shorter than the VIII-group females.

male rock bass attain legal length approximately a year earlier than do the females (p. 222) and hence are subjected to mortality from fishing at an earlier age. On the other hand, it should be pointed out that the changes in the sex ratio were most pronounced at the later ages when the individuals of both sexes were well above legal size and a differential destruction in the fishery logically could not be expected. It is true also that the mortality from the very limited sport fishery was negligible.⁵³

The selective destruction of the sexes by predators should cause the relative abundance of females to decrease rather than to increase with increase in age, since the more rapid growth of the males should carry them first to a size at which they are no longer subject to attack by larger fish. The size at which the Nebish Lake rock bass becomes too large to be attacked by predators is probably small. The only other species taken in abundance by the gill nets were perch and smallmouth black bass (p. 328).

The failure of other possible causes to explain the observed changes in the sex ratio leads to the conclusion that the inherent viability of females is greater than that of males. This conclusion that females enjoy the longer natural life span is in agreement with certain other investigations. Geiser (1923, 1924 a, b) held that a differential mortality of the sexes is general among animals, and that ordinarily the females are more viable than the males.⁵⁴ He cited numerous examples from literature to show that the relative mortality of the males is especially high under adverse conditions. Hile (1936a) believed that environmental conditions had an important effect on the sex ratios of the cisco populations of four northeastern Wisconsin lakes. In support of this belief he called attention to the fact that the four stocks followed "the same order with respect to growth in weight

⁵³ Prior to 1934, Nebish Lake was very difficult of access. It could be reached only by means of narrow and rough "woods road" that followed the road-bed of a former lumber railway line.

⁵⁴ In the 1924b publication Geiser stated that there is "a direct relation demonstrated between the greater longevity (of the sexes) in animals and the possession of a duplex condition of the sex-determining chromosomes." Females would then be expected usually to have the longer lives because of the more common occurrence of the XX, XY type of sex chromosomes. Among the birds whose sex chromosomes are of the WW, WZ type the males live longer than the females.

and the average relative abundance of males", and concluded, "that the less viable males probably suffer greater mortality under adverse conditions that produce slow growth, and hence that the correlation between growth rate and sex ratio may be considered to result from the dependence of these two characteristics on the same environmental factors."

Sex differences in the rate of natural mortality do not provide the explanation for all of the changes of sex ratio with increase in age that have been observed. In the presence of an intensive fishery, sex differences in the age of entry into the fishery may have an important effect on the relationship between the sex ratio and age. Van Oosten (1929) who found that females exceeded the males in number in the younger age groups of the Lake Huron herring but were in the minority at the higher ages, attributed the shifting sex ratio to the earlier attainment of sexual maturity by the females and the consequent tendency for them to appear in and be destroyed by the commercial fishery at an earlier age. The same author (Van Oosten, 1939) believed that the lower age at maturity of the male Lake Huron whitefish led to their destruction in the fishery at an earlier age and thus accounted for the relative scarcity of males in the older age groups. Willer (1925) suggested that the sex ratio of the European lake herring (*Coregonus albula*) may be affected by selective destruction by predators, correlated with sex differences in size.

SPECIES ASSOCIATED WITH THE NEBISH LAKE ROCK BASS

The only species taken with the rock bass in the gill-net collections from Nebish Lake, 1930 to 1932, were the yellow perch, the smallmouth black bass, and the largemouth black bass (Table 64). The hook-and-line catches contained rock bass, perch, and smallmouth black bass but included no largemouth bass.

Over the 3-year period rock bass were approximately twice as abundant in the gill-net catches as perch and seven times as abundant as smallmouth black bass. The number of largemouth black bass was insignificant (only 2 fish in a total of 1,923). It is unlikely that Nebish Lake was supporting a population of largemouth bass at the time of the collections. More probably

the two small specimens taken in 1932 had been introduced. The data of Table 64 give some indication that the proportion of perch in the Nebish Lake fish stock may have been on the increase over the period, 1930 to 1932.

TABLE 64. *Species composition of gill-net catches in Nebish Lake, 1930-1932. In parentheses, catches of species other than rock bass expressed as percentages of the number of rock bass captured in the same year or years.*

Year of capture	Species			
	Rock bass	Yellow perch	Smallmouth black bass	Largemouth black bass
1930	144 ..	348 (33)	8 (6)	
1931	513 ..	213 (42)	85 (17)	
1932	492 ..	353 (72)	65 (13)	2 (0) ¹
Total	1,149 ..	614 (53)	158 (14)	2 (0) ¹

¹ Less than 0.5 per cent.

The number of fish in Table 64 should not be taken as indicative of the relative abundance of the species in the lake since the comparative facility with which gill nets capture the three species is unknown. The yellow perch, with its more slender form, might be expected to gill more readily than rock bass. On the other hand, there is reason to believe that smallmouth black bass may avoid gill nets, particularly if the webbing is light-colored. The introduction of more darkly colored nets was found to bring about an immediate increase in the catch of smallmouth bass.

Detailed information concerning the bathymetric distribution of rock bass, perch, and smallmouth black bass in Nebish Lake (presented by Hile and Juday in a paper appearing simultaneously with this report) reveals that to a large extent the three species occupy a common habitat in late July and early August. The only indication of segregation was detected in the tendency for the larger rock bass to occupy slightly deeper water than did perch, smallmouth black bass, and the smaller rock bass.

SUMMARY

1. The investigation of the Nebish Lake rock bass was based on data from 1,453 specimens. Ages were determined and growth histories were calculated for 1,215 individuals.

2. The validity of the annulus on rock bass scales as a true year-mark was established by the following observations:

(a) Fish assigned to the same age group have similar lengths.

(b) There was agreement between the age of small fish as estimated from length-frequency distributions and from scale examinations.

(c) Lengths calculated from scale measurements agreed well with the empirical lengths of younger age groups, including age groups whose ages were established from length-frequency distributions.

(d) Calculated lengths for corresponding years of life agreed well among fish of the same or different ages, but the agreement among different age groups of the same year class was better than among age groups of different year classes.

(e) Calculated growth histories for different age groups and different year classes agreed in showing growth to have been good or poor in certain calendar years.

(f) Certain year classes were persistently abundant or poorly represented in the collections of successive years.

3. Accessory or false annuli were a minor source of difficulty in the determination of age. The erosion of portions of the scale led to the rejection of the scales from a limited number of older rock bass.

4. The mathematical relationship between body length (L) and the length of the anterior radius of the magnified scale (S) was described satisfactorily by the equation:

$$L = 5.84011 S^{0.695992}$$

Computations of individual growth histories were made with the assistance of a table of solutions of this equation.

5. The average lengths and weights of the age groups tended to increase from 1930 to 1932. In 1935 most age groups aver-

aged shorter but heavier than the corresponding age groups of the 1932 collection.

6. The length-frequency distributions of the successive age groups ordinarily exhibited large overlap. Fish of the same length interval were represented in as many as six age groups. Only age-group II formed a distinct mode in the frequency distribution for all ages combined.

7. The youngest age groups with grand average lengths above the legal size limit of 7 inches, total length, (146 millimeters, standard length) were age-group V of the males and age-group VI of the females.

8. Where the number of specimens was large the calculated lengths of different age groups of the same year class agreed well. The growth histories of the year classes, however, exhibited rather large variations. These variations were sufficiently great to cause significant changes from one calendar year to another in the relationship of size to age.

9. The general growth curves for the population show that males grow more rapidly than females. The differential growth of the sexes is not distinctly apparent before the fourth year.

10. The rock bass grows more rapidly in Nebish Lake than in two neighboring lakes, Muskellunge Lake and Trout Lake, but much more slowly than in Lake Wawasee and Syracuse Lake in northern Indiana.

11. The growth of the Nebish Lake rock bass is subject to rather large annual fluctuations. The extremes of variation in the growth of rock bass beyond the first year of life occurred in 1931 when growth was 20.6 per cent above the 1922-1931 average and in 1928 when growth was 15.2 per cent below average. Annual fluctuations in first-year growth appear to be independent of fluctuations in the growth of older fish.

12. The strength of year classes also is subject to wide fluctuations. Exceptionally strong year classes were produced in 1923 and 1930. Year classes were very weak in the four years, 1925 to 1928.

13. In general, strong year classes occurred in years of good growth (in the second and later years of life) and weak year classes in years of poor growth. First-year growth, however,

was not correlated with growth in later years or with fluctuations in the strength of year classes.

14. The annual fluctuations in growth in the second and later years of life and the strength of year classes of the Nebish Lake rock bass exhibited correlations with variations in temperature and precipitation.

15. Good growth was correlated positively with high temperatures, especially in June and September. It was suggested that the temperature of these two months may determine annual fluctuations in the length of the growing season. Good growth and heavy precipitation in June also were correlated positively.

16. The occurrence of strong year classes in the rock bass of Nebish Lake was correlated with high temperatures and heavy rainfall in early season (May, June, and July), conditions in June being particularly significant.

17. The correlation between rainfall and the fluctuations in growth and the strength of year classes may depend on the enrichment of this oligotrophic lake by materials washed in during periods of heavy downpour. Temperatures may have a direct effect on the physiological processes of the fish or may affect the abundance of fish food in the lake.

18. Variations from year to year in population density, dependent on fluctuations in the strength of the year classes produced in earlier years, possibly may have an important effect on annual fluctuations in growth and in the survival of young.

19. For comparison, data were presented on the relationship between meteorological conditions and annual fluctuations in the growth and the strength of the year classes of the rock bass populations in the two neighboring lakes, Muskellunge Lake and Silver Lake, and on the strength of the year classes in Trout Lake.

20. The growth of the Muskellunge Lake rock bass was correlated closely with annual fluctuations in temperature. The coefficient of correlation between annual deviations in growth and June temperature was 0.75. No significant correlation could be demonstrated between growth and precipitation or between the strength of year classes and temperature or precipitation.

21. The limited data for the Silver Lake rock bass indicated annual fluctuations in growth rate somewhat similar to those of

the Nebish Lake rock bass. The occurrence of a strong year class in 1925 and possibly in 1928 disagreed with the Nebish Lake data.

22. Agreements such as those indicated by the existence of a positive correlation between temperature and the growth of rock bass in both Nebish Lake and Muskellunge Lake (and probably in Silver Lake also) and by the simultaneous occurrence of strong year classes of rock bass in 1923 in Nebish Lake, Muskellunge Lake, and Trout Lake point toward a common effect of weather conditions on the rock bass populations of the area. Other observations indicate that, in certain years at least, conditions peculiar to the individual lakes may play a dominant rôle. The growth fluctuations of the rock bass in Nebish Lake and Muskellunge Lake both were correlated significantly with temperature but were, themselves, weakly correlated ($r = 0.38$). Furthermore, the 1928 year class was strong in Muskellunge Lake (and probably in Silver Lake) but extremely weak in Nebish Lake, and the 1925 year class was exceptionally rich in Silver Lake but relatively poor in both Nebish Lake and Muskellunge Lake.

23. The greater part of the season's growth had been completed at the time of capture in late July and early August. At capture the older rock bass had completed a lesser percentage of the season's growth than had younger fish, and males had completed a smaller percentage of the season's growth than had females.

24. The superior late-season growth of the males accounts in large measure for the generally more rapid growth of rock bass of that sex.

25. The relationship between the length at the end of the first year of life and growth in later years is subject to considerable variation. First-year advantage in size may be retained over 1 or 2 additional years, but more probably it will be increased in the second and/or third year of life. Compensatory growth occurs in the later years.

26. The observed relationship between first-year length and later growth in length may be to some extent an "apparent" phenomenon traceable to differences in the age (time of hatching in the season of origin) of individuals. Nevertheless there are

also conclusive arguments for the existence of growth compensation as a real as well as an "apparent" phenomenon.

27. Male rock bass were slightly heavier than females of corresponding length in the collection of July 5 and 6, 1930, but females were slightly heavier than males in the combined collections of late July and early August, 1930 to 1932. No sex differences were found in the weights of fish of corresponding length in the collection of August 28, 1935.

28. Rock bass captured in 1935 were much heavier for their length than were fish captured in earlier years. However, the 1935 collection was taken later in the season than were the collections of previous years. Since fish captured earlier in the season (late July and early August) in three consecutive years (1930 to 1932) exhibited only small differences in the length-weight relationship, the high weights of the 1935 specimens may represent a seasonal rather than an annual fluctuation.

29. The mathematical relationship between the standard length in millimeters (L) and the weight in grams (W) of rock bass captured in late July and early August, 1930 to 1932, (sexes combined) was described satisfactorily by the equation:

$$W = 2.884 \times 10^{-5} L^{3.003}$$

This equation approximates the cubic parabola very closely.

30. The coefficient of condition, K , increased irregularly with an increase in age. Female rock bass of the 1930-1932 collections tended to have slightly higher values of K than male rock bass of the same age.

31. The first spawning of the rock bass may occur as early as the beginning of the fourth year of life (end of third) or as late as the beginning of the seventh year of life (end of sixth). The age at which a majority was mature varied in the different years' collections. Males and females mature at approximately the same age. The legal size limit of 7 inches affords full protection to immature fish.

32. The rate of growth affects the time of attainment of maturity. An age group that has grown rapidly may contain a higher percentage of mature fish than an older age group in which the fish are of greater average size but have grown slowly.

The mature individuals of an age group ordinarily average longer than immature fish of the same age.

33. Females were more abundant than males in each year's collection. The relative abundance of females increased irregularly with increase in age. The greater relative abundance of females in the older age groups indicates the existence of a differential natural mortality of the sexes.

34. The gill-net collections of 1930 to 1932 included 614 yellow perch, 158 smallmouth black bass, and 2 largemouth black bass in addition to the 1,149 rock bass.

LITERATURE CITED

- Bennett, George W. 1937. The growth of the large mouthed black bass, *Huro salmoides* (Lacépède), in the waters of Wisconsin. *Copeia* 1937 (2):104-118.
- Bennett, George W. 1938. Growth of the small-mouthed black bass, *Micropterus dolomieu* Lacépède, in Wisconsin waters. *Copeia* 1938 (4):157-170.
- Couey, Faye M. 1935. Fish food studies of a number of northeastern Wisconsin lakes. *Trans. Wis. Acad. Sci., Arts and Let.* 29:131-172.
- Cross, Samuel X. 1934. A probable case of non-specific immunity between two parasites of ciscoes of the Trout Lake region of northern Wisconsin. *Jour. Parasitol.* 20 (4):244-245.
- Cross, Samuel X. 1935. The effect of parasitism on growth of perch in the Trout Lake region. *Jour. Parasitol.* 21 (4):267-273.
- Cross, Samuel X. 1938. A study of the fish parasite relationships in the Trout Lake region of Wisconsin. *Trans. Wis. Acad. Sci., Arts and Let.* 31:439-456.
- Evermann, Barton Warren and Howard Walton Clark. 1920. Lake Maxinkuckee. A physical and biological survey. Department of Conservation, State of Indiana, Publication No. 7. 2 vols. 660 + 512 pp.
- Forbes, Stephen Alfred and Robert Earl Richardson. 1920. The fishes of Illinois. Second Edition. *Nat. Hist. Survey of Illinois*, Vol. III, cxxxvi + 357 pp.
- Ford, E. 1933. An account of the herring investigations conducted at Plymouth during the years from 1924 to 1933. *Jour. Marine Biol. Assoc. United Kingdom* 19(1):305-384.
- Geiser, S. W. 1923. Evidences of a differential death rate of the sexes among animals. *Amer. Mid. Nat.* 8 (7):153-163.
- Geiser, S. W. 1924a. Sex ratios and spermatogenesis in the top-minnow, *Gambusia holbrooki* Grd. *Biol. Bul.* 47 (3):175-212.

- Geiser, S. W. 1924b. The differential death rate of the sexes among animals, with a suggested explanation. Wash. Univ. Stud. 12 (Series 1):73-96.
- Goulden, C. H. 1939. Methods of statistical analysis. John Wiley and Sons, Inc. vii + 277 pp.
- Graham, Michael. 1929. Studies of age-determination in fish. Part II. A survey of the literature. Min. Agric. and Fish., Fish. Invest. Ser. II, 11 (3): 50 pp.
- Greeley, J. R. 1930. A biological survey of the Champlain watershed. II. Fishes of the Lake Champlain watershed. N. Y. Cons. Dept., Sup. 19th An. Rept.: 44-87.
- Greeley, John R. and C. Willard Greene. 1931. A biological survey of the St. Lawrence watershed. II. Fishes of the area. N. Y. Cons. Dept., Sup. 20th An. Rept.: 44-94.
- Greene, C. Willard. 1935. The distribution of Wisconsin fishes. State of Wisconsin, Conservation Commission. 235 pp.
- Hile, Ralph. 1931. The rate of growth of fishes of Indiana. Investigations of Indiana Lakes, No. 2, Ind. Dept. Cons., Pub. No. 107:7-55.
- Hile, Ralph. 1936a. Age and growth of the cisco, *Leucichthys artedi* (Le Sueur), in the lakes of the northeastern highlands, Wisconsin. Bul. Bur. Fish. 48:211-317.
- Hile, Ralph. 1936b. Summary of investigations on the morphometry of the cisco, *Leucichthys artedi* (Le Sueur), in the lakes of the northeastern highlands, Wisconsin. Papers Mich. Acad. Sci., Arts and Let. 21 (1935):619-634.
- Hile, Ralph. 1937. Morphometry of the cisco, *Leucichthys artedi* (Le Sueur), in the lakes of the northeastern highlands, Wisconsin. Internat. Rev. ges. Hydrobiol. u. Hydrog. 36:57-130.
- Hile, Ralph and Hilary J. Deason. 1934. Growth of the whitefish, *Coregonus clupeaformis* (Mitchill), in Trout Lake, northeastern highlands, Wisconsin. Trans. Amer. Fish. Soc. 64:231-237.
- Hodgson, William C. 1929. Investigations into the age, length, and maturity of the herring of the southern North Sea. III. The composition of the catches from 1923 to 1928. Min. Agric. and Fish., Fish. Invest. Ser. II, 11(7):71 pp.
- Hubbs, Carl L. and Gerald P. Cooper. 1935. Age and growth of the long-eared and the green sunfishes in Michigan. Papers Mich. Acad. Sci., Arts and Let. 20 (1934): 669-696.
- Jordan, David Starr and Barton Warren Evermann. 1896. The fishes of North and Middle America. Part I. Bul. U. S. Nat. Mus. No. 47, lx + 1240 pp.

- Juday, Chancey and George W. Bennett. 1935. Growth of game fish in Wisconsin waters. Third report. Notes from the Limnological Laboratory of the Wisconsin Geological and Natural History Survey. May, 1935. 13 pp. Mimeographed.
- Juday, C. and E. A. Birge. 1930. The highland lake district of northeastern Wisconsin and the Trout Lake limnological laboratory. *Trans. Wis. Acad. Sci., Arts and Let.* 25:337-352.
- Juday, Chancey and Clarence L. Schloemer. 1936. Growth of game fish in Wisconsin waters. Fourth report. Notes from the Limnological Laboratory of the Wisconsin Geological and Natural History Survey. June, 1936. 17 pp. Mimeographed. Fifth report. April, 1938. 26 pp. Mimeographed.
- Juday, Chancey and Edward Schneberger. 1930. Growth studies of game fish in Wisconsin lakes. Notes from the Limnological Laboratory of the Wisconsin Geological and Natural History Survey. March, 1930. 7 pp. Mimeographed. Second report. April, 1933. 10 pp. Mimeographed.
- Monastyrsky, G. N. 1930. Über Methoden zur Bestimmung des linearen Wachstums des Fische nach der Schuppe. *Rept. Sci. Inst. Fish Cult.* 5(4):5-44. [Russian with German summary.]
- Morgulis, Sergius. 1912. Studien über Inanition in ihrer Bedeutung für das Wachstumsproblem. II. Experiments an *Triton cristatus*. *Archiv f. Entwicklunsm. d. Org.* 34:618-679.
- Osborne, Thomas B. and Lafayette B. Mendel. 1915. The resumption of growth after long continued failure to grow. *Jour. Biol. Chem.* 23:439-454.
- Schloemer, Clarence L. 1936. The growth of the muskellunge, *Esox masquinongy immaculatus* (Garrard), in various lakes and drainage areas of northern Wisconsin. *Copeia* 1936 (4):185-193.
- Schloemer, Clarence L. 1938. A second report on the growth of the muskellunge, *Esox masquinongy immaculatus* (Garrard), in Wisconsin waters. *Trans. Wis. Acad. Sci., Arts and Let.* 31:507-512.
- Schneberger, Edward. 1935. Growth of the yellow perch (*Perca flavescens* Mitchill) in Nebish, Silver and Weber lakes, Vilas County, Wisconsin. *Trans. Wis. Acad. Sci., Arts and Let.* 29:103-130.
- Segerstråle, Curt. 1933. Ueber scalimetrische Methoden zur Bestimmung des linearen Wachstums bei Fischen, insbesondere bei *Leuciscus idus* L., *Abramis brama* L., und *Perca fluviatilis* L. *Acta Zoolog. Fennica* 15:1-168.
- Spoor, William A. 1938. Age and growth of the sucker, *Catostomus commersonnii* (Lacépède), in Muskellunge Lake, Vilas County, Wisconsin. *Trans. Wis. Acad. Sci., Arts and Let.* 31:457-505.
- Springer, Ada. 1909. A study of growth in the salamander, *Diemyctylus viridescens*. *Jour. Exp. Zool.* 6(1):1-68.

- Thompson, Helen B. and Lafayette B. Mendel. 1918. An experimental study of alternating growth and suppression of growth in the albino mouse, with special reference to the economy of food consumption. *Amer. Jour. Physiol.* 45(4):431-458.
- Titcomb, John W., Eben W. Cobb, Mary F. Crowell, and C. M. McCay. 1928. The nutritional requirements and growth rates of brook trout. *Trans. Amer. Fish. Soc.* 58:205-231.
- Van Oosten, John. 1923. The whitefishes (*Coregonus clupeaformis*). A study of the scales of whitefishes of known ages. *Zoologica* 2(17):380-412.
- Van Oosten, John. 1929. Life history of the lake herring (*Leucichthys artedi* Le Sueur) of Lake Huron as revealed by its scales, with a critique of the scale method. *Bul. Bur. Fish.* 44:265-428.
- Van Oosten, John. 1937. The age, growth, and sex ratio of the Lake Superior longjaw, *Leucichthys zenithicus* (Jordan and Evermann). *Papers Mich. Acad. Sci., Arts and Let.* 22 (1936):691-711.
- Van Oosten, John. 1938. The age and growth of the Lake Erie sheepshead, *Aplodinotus grunniens* Rafinesque. *Papers Mich. Acad. Sci., Arts and Let.* 23 (1937):651-668.
- Van Oosten, John. 1939. The age, growth, sexual maturity, and sex ratio of the common whitefish, *Coregonus clupeaformis* (Mitchill), of Lake Huron. *Papers Mich. Acad. Sci., Arts and Let.* 24(2) (1938): 195-221.
- Van Oosten, John, H. J. Deason and Frank W. Jobes. 1934. A micro-projection machine designed for the study of fish scales. *Jour. du Cons.* 9(2):241-248.
- Viosca, Percy, Jr. 1936. A new rock bass from Louisiana and Mississippi. *Copeia* 1936(1):37-45.
- Willer, A. 1925. Das Laichgeschäft der kleinen Maräne in Ostpreussen. *Internat. Rev. ges. Hydrobiol. u. Hydrog.* 12:313-332.
- Wright, Stillman. 1929. A preliminary report on the growth of the rock bass, *Ambloplites rupestris* (Rafinesque), in two lakes of northern Wisconsin. *Trans. Wis. Acad. Sci., Arts and Let.* 24:581-595.
- Zabinski, Jan. 1929. The growth of blackbeetles and of cockroaches on artificial and on incomplete diets. Part I. *British Jour. Exp. Biol.* 6(4):360-386.

AGE, GROWTH, AND PRODUCTION OF THE YELLOW PERCH, *PERCA FLAVESCENS* (MITCHILL), OF SAGINAW BAY

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ABSTRACT

Ages were determined and individual growth histories computed from the examination and measurement of scales from 820 yellow perch collected in 1929 and 1930. Calculated lengths greater than 101 millimeters were computed on the assumption (supported by empirical data) that the ratio of body length to scale length is constant. Lengths below 101 millimeters were determined with the aid of an empirical curve of the body-scale relationship of small fish.

Yellow perch of age-groups III and IV (in the fourth and fifth years of life) made up the bulk of the collection (78 per cent). Females grew slightly more rapidly than males, but members of both sexes attained the legal length of 8½ inches during the fourth year of life, just as they were entering on the period of most rapid growth in weight. The greatest growth in weight of both sexes occurred in the sixth year of life. In the combined samples of the two years the females exceeded the males in abundance in the ratio, 296:100.

The weight of the Saginaw Bay yellow perch was found to increase as the 3.117 power of the length. The relative length of the tail decreased with increase in the length of the fish.

The Saginaw Bay yellow perch is now far less abundant than it was in the early years of the fishery. The average annual production of 548,000 pounds over the period, 1917-1938, was only 28 per cent of the earlier (1891-1916) "normal" annual production of 1,961,000 pounds. A detailed analysis of statistical data available for more recent years made possible a description of annual fluctuations in the abundance and production of yellow perch and in the intensity of the yellow perch fishery in Saginaw Bay over the period, 1929-1938.

INTRODUCTION

The yellow perch, *Perca flavescens* (Mitchill), is one of the most common and most highly prized of the fresh-water fishes of the north-eastern United States and southeastern Canada. The species finds favor with anglers both because of its excellent quality and because of the ease with which it may be captured. Yellow perch taken in the commercial fishery ordinarily find a ready market at a good price.

Saginaw Bay is the most important center of commercial production of yellow perch in the State of Michigan waters of the Great Lakes and, next to Lake Erie, contains the most productive perch grounds in the entire Great Lakes. The yellow perch is not, however, the leading species in the commercial fishery of the Bay. During the years, 1934-1938, the average annual catch of perch in Saginaw Bay was exceeded by the catches of lake herring, wall-eyed pike, suckers, and carp, in that order of importance.

Numerous studies have been made of the age and growth of perch in small inland lakes, but to date only two publications have appeared dealing with the growth of perch in Great Lakes waters. Both of

these small papers (Harkness, 1922; Jobes, 1933) were concerned with the Lake Erie yellow perch. A comprehensive life-history study of the Lake Erie perch (Jobes, MS.) will be published in the near future. Nothing has been published concerning the growth of the yellow perch of Lake Huron.

MATERIALS AND METHODS

The investigation of the age and growth of the Saginaw Bay yellow perch has been based on the examination and measurement of the scales of 820 fish taken by experimental pound nets (mesh sizes—2, 2½, 2¾, and 3 inches, stretched measure as manufactured) during the spring and early summer fishing seasons of 1929 and 1930. These nets were set near Sand Point, north of Bayport, Michigan. The study of the length-weight relationship was made from the data for 1,483 perch captured in experimental pound nets near Sand Point in the years, 1928-1930, and in commercial trap nets off Bay City, Michigan, in 1934. The relationship between total length and standard length was determined from measurements of 1,411 fish collected in the same 4 years and from the same nets. Scattered collections totalling 512 fish captured at various times in the season from April to November in the years, 1921, 1925-1927, 1930, and 1934 were employed for the investigation of the relationship between body length and the anterior interradial measurement of the scale. Of these 512 perch, 332 were taken by small hand seines, mostly along the south shore of the Bay. The remaining 180 fish were captured by commercial trap nets off Bay City.

All fish except 332 preserved specimens used in the study of the body-scale relationship were weighed and measured when fresh. Lengths were measured with a steel tape and were recorded to the nearest millimeter. Weights were recorded to the quarter ounce. The preserved fish were not weighed; their lengths were corrected for shrinkage by the factor, 1.005, which has been determined empirically.

The scales employed for age determinations were mounted on standard 3- by 1-inch microscope slides in a glycerin-gelatine medium and were examined and measured on a micro-projection apparatus at the magnification, X 40.7. Ages were designated by Roman numerals corresponding to the number of annuli on the scales. For example, yellow perch with one annulus (in the second year of life) are members of age-group I.

COMMERCIAL PRODUCTION OF YELLOW PERCH IN SAGINAW BAY

Data are available on the commercial production of perch in Saginaw Bay for the 18 years, 1891-1908, and for the 23 years, 1916-1938¹

¹The records for the years, 1891-1908 and 1929-1938, were compiled from State of Michigan records on file in the Great Lakes laboratory of the Fish and Wildlife Service. The data for the remaining years were obtained from the following reports published by the State of Michigan: 1916-1919, biennial reports of the State Game, Fish and Forest Fire Department of the Public Domain Commission; 1920-1928, biennial reports of the Department of Conservation.

Table 1.—Annual production of yellow perch in Saginaw Bay, 1891-1908 and 1916-1938

Year	Production (pounds)	Year	Production (pounds)
1891	1,102,650	1920	803,725
1892	1,801,600	1921	659,254
1893	1,691,600	1922	461,111
1894	2,013,500	1923	572,817
1895	1,754,300	1924	444,064
1896	1,577,300	1925	414,137
1897	1,539,000	1926	314,848
1898	2,187,650	1927	112,711
1899	2,804,200	1928	192,008
1900	3,452,800	1929	441,373
1901	3,379,200	1930	611,679
1902	2,384,500	1931	655,542
1903	2,069,200	1932	587,532
1904	1,529,200	1933	330,877
1905	1,571,700	1934	398,555
1906	1,747,900	1935	836,784
1907	1,935,000	1936	1,073,861
1908	1,085,877	1937	351,382
1916	1,637,691	1938	326,824
1917	642,840	Average, 1891-1938	1,203,204
1918	789,287	Average, 1891-1916	1,961,309
1919	1,018,292	Average, 1917-1938	548,477

(Table 1). On the basis of the available statistics it is possible to speak of an early period of high production (1891-1916) and of a recent period of relatively low yield (1917-1938). The annual production fell below 1,500,000 pounds only twice (1891 and 1908) in the former period, and exceeded 2,000,000 pounds in 7 of the 19 years for which there are records. In the latter period, however, the commercial catch rose above 1,000,000 pounds only twice (1919 and 1936) in 22 years and was less than 500,000 pounds in 11 years.

Production was by no means uniform within the two periods. In the earlier period, for example, the annual catch was consistently above 2,000,000 pounds for the 6 consecutive years, 1898-1903, and was above 3,000,000 pounds in both the record year of 1900 and in 1901. By comparison the catch was relatively low in certain other periods, as 1895-1897 and 1904-1906. In the recent period, 6 consecutive years (1924-1929) had productions below 500,000 pounds, whereas the catch was relatively much higher in other years (1918-1920, 1935-1936). These fluctuations do not, however, invalidate the separation of the history of production into an early and a modern period.

The extent to which the production of yellow perch in Saginaw Bay has fallen off since 1916 can be brought out more clearly by comparisons in which recent catches are expressed as percentages of the earlier or "normal" yield. If the average 1891-1916 catch is given the value of 100, the average annual yield for the 22 years, 1917-1938, may be determined as 28. The annual production of the modern fishery is therefore 72 per cent below the early "normal." Even the excellent catch of 1936 was only 55 per cent of the normal. The average production for the most recent 10-year period, 1929-1938, in spite of good years in 1935 and 1936, was only 29 per cent of normal.

Table 2.—Production of yellow perch in Saginaw Bay, 1929-1938, according to gear and total production and fishing intensity in each year, expressed as a percentage of the 1929-1934 average

Year	Production in pounds by gear						Production as percentage of 1929-1934 average	Fishing intensity as percentage of 1929-1934 average
	Small-mesh gill net	Pound net	Shallow trap net	Fyke net	Seine	All others ¹		
1929	25,689	54,985	269,132	46,524	27,241	17,802	88	78
1930	74,171	51,262	383,059	63,104	37,332	2,751	121	111
1931	74,277	47,358	431,454	68,492	29,784	4,177	130	134
1932	28,351	22,754	439,539	64,695	16,269	15,924	116	96
1933	10,855	16,651	264,937	28,466	8,625	1,343	66	94
1934	7,096	17,665	335,623	16,499	10,965	10,707	79	87
1935	122,473	17,266	627,040	35,990	22,305	11,710	166	129
1936	256,970	15,766	743,668	25,704	24,307	7,446	213	158
1937	23,696	4,929	254,792	41,231	25,414	1,320	70	104
1938	4,787	4,963	266,076	33,490	16,574	934	65	88
Average	62,836	25,360	401,532	42,420	21,882	7,411	...	...
Percentage	11.2	4.5	71.5	7.6	3.9	1.3	...	...
							441,373	78
							611,679	121
							655,542	130
							587,532	116
							330,877	66
							398,555	79
							836,784	166
							1,073,861	213
							351,382	70
							326,824	65
							561,441	...
								...

¹Includes the catches from large-mesh gill nets, deep trap nets, hooks, and spearing as well as catches for which records of gear were not available.

Table 3. Catch of yellow perch per unit fishing effort of five gears over the period, 1929-1938, and the annual fluctuations in the abundance of yellow perch expressed as percentages of the 1929-1934 average

Year	Catch in pounds per unit effort in gear					General abundance
	Small-mesh gill net	Pound net	Shallow trap net	Fyke net	Seine	
1929	45.71	6.46	17.75	5.61	30.02	110
1930	14.61	7.37	17.91	10.19	22.02	110
1931	9.74	6.72	16.54	10.51	22.34	98
1932	15.59	6.63	19.28	12.22	19.87	121
1933	8.66	2.93	11.50	7.04	14.95	71
1934	7.85	4.16	14.70	6.08	26.96	90
1935	12.20	3.83	23.98	12.04	51.60	125
1936	15.70	5.36	26.20	6.59	41.64	133
1937	4.99	3.38	10.68	9.32	43.52	66
1938	3.78	3.56	11.91	7.06	34.06	73
Average, 1929-1934	17.03	5.71	16.28	8.61	22.69	100

The low production of yellow perch in Saginaw Bay since 1916 cannot be attributed to a relaxation of fishing effort. On the contrary, it is conceded generally that the fishing intensity of recent years is far greater than it was in the earlier years of the fishery. Consequently, the low production of the present-day fishery must be recognized as the result of a reduction in the density of the population. Although a detailed consideration of the causes of the depletion of the yellow perch population of Saginaw Bay does not come within the scope of this paper, it can be stated safely that over-fishing probably played a dominant role. Pollution also may have been an important factor.

The detailed records of daily fishing activities that must be submitted at the end of each month by every commercial fisherman licensed to operate in the State of Michigan waters of the Great Lakes make possible the presentation of data for the years, 1929-1938, relative to the composition of the catch of yellow perch according to the gear of capture and to the annual fluctuations in production, fishing intensity, and the abundance of fish on the grounds (Tables 2 and 3). From Table 2 it may be seen that the shallow trap net now accounts for the greater portion of the catch. This gear not only took 71.5 per cent of the total catch in the 10 years, but computations of percentages for the individual years reveal that in 3 years (1933, 1934, and 1938) trap nets took more than 80 per cent of the total, and that in no year did they take less than 61 per cent. The remaining gears in the order of their importance for the production of perch were as follows: Small-mesh gill nets, fyke nets, pound nets, and seines. However, the relative importance of these minor gears varied considerably from year to year. For example, the percentage of the total catch produced by small-mesh gill nets ranged from 23.9 per cent in 1936 to 1.5 per cent in 1938. The annual variations in the percentage of perch taken in pound nets, fyke nets, and seines were somewhat less extensive.

The different gears showed only fair agreement with respect to the annual fluctuations in the quantity of yellow perch taken per unit fishing effort.² As illustrations, the lifts of pound nets were not benefited by the increase in general abundance that occurred in 1935, and the catches of both fyke nets and seines failed to suffer from the great decline in abundance in 1937. These disagreements are not surprising since the production of yellow perch in gears other than the shallow trap net is normally so small that considerable random variation in the catch per unit of effort may be expected.

Total production, fishing intensity, and the abundance³ of fish on the grounds were subject to considerable annual fluctuation (Tables 2 and 3; Fig. 1). Of the three, production was the most variable. The maximum production was more than three times the minimum whereas the maxima of the intensity and abundance percentages were about twice the minima. The greater range of variation of production arises from the circumstance that the simultaneous occurrence of maxima of both fishing intensity and abundance in 1936 led to an exceptionally high yield in that year. Fishing intensity was above average in the year of lowest abundance (1937) and abundance was above average in the year of lowest fishing intensity (1929). In 1938, however, both abundance and fishing intensity were sufficient below average to carry production to the low level of 65 per cent of average.

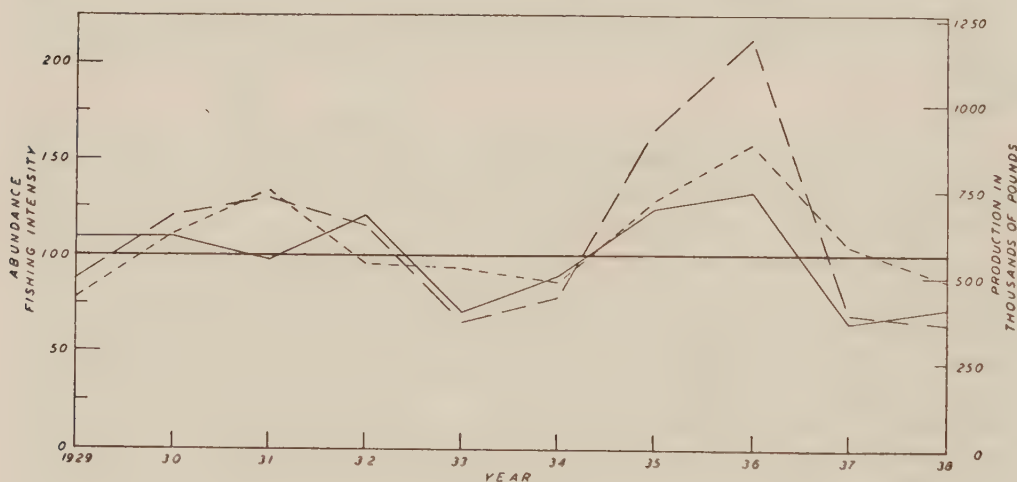


Figure 1.—Annual fluctuations in the abundance ———, and production — — — of yellow perch, and in the intensity of the fishery for perch - - - in Saginaw Bay, expressed as percentages of the 1929-1934 average.

²The units of effort for the various gears are as follows: Small-mesh gill nets—the lift of 1,000 linear feet; pound nets, shallow trap nets, and fyke nets—the lift of one net; seines—one haul of a 100-rod seine.

³The method of computing general abundance was outlined by Hile (1937). The fishing intensity in a particular year is the catch that would be expected from the amount of gear fished if abundance were exactly normal, expressed as a percentage of the mean of the "expected" catches in the years, 1929-1934. This 6-year period has been taken tentatively as the "normal" or "period of reference" for the study of fluctuations in the modern commercial fisheries of the Great Lakes waters of the State of Michigan.

BODY-SCALE RELATIONSHIP AND THE CALCULATION OF GROWTH

The method employed in this study for the calculation of individual growth histories of Saginaw Bay yellow perch from scale measurements was determined by a study of "key" or selected scales from 512 individuals, collected at various dates from April to November in the years 1921, 1925-1927, 1930, and 1934. The relationship between body length and the measurements of the anterior interradi spaces of these key scales⁴ may be found in Table 4. (See also Fig. 2.)

The values of the body-scale ratio (L/Sc) in Table 4 demonstrate that among the smaller yellow perch the relative size of the scale increases with increase in the length of the fish. This increase in the relative size of the scales of these larger fish is brought out in Figure 2 of about 90 millimeters, beyond which point the body-scale ratio remains nearly constant. The limited extent of the variations in the relative size of the scale comes to an end, however, at a body length by the closeness with which the line, $L = 1.24 Sc$, (1.24 is the grand average value of the body-scale ratio of perch more than 90 millimeters long) fits the empirical averages of body lengths (L) and scale measurements (Sc). The most notable discrepancies occur beyond the length of 200 millimeters. Even these discrepancies are not great and the numerical representation of the larger fish was relatively weak. It appears valid, therefore, to assume that the body-scale ratio is constant at all lengths beyond 90 millimeters.

Direct-proportion computations may be used for the calculation of lengths that are greater than the length at which the body-scale ratio

Table 4.—Relationship between body length (L) and the anterior interradi measurement (Sc) of "key" or selected scales of Saginaw Bay yellow perch

Number of fish	Standard length (millimeters)	Scale length (millimeters X 40.7)	Average L/Sc ratio
20	48.4	26.6	1.82
98	55.4	31.8	1.74
83	64.2	40.9	1.57
20	73.9	52.4	1.41
24	84.9	63.8	1.33
27	94.1	74.0	1.27
18	104.3	82.4	1.27
13	114.4	92.9	1.23
7	123.6	101.9	1.21
16	134.4	107.7	1.25
27	145.9	117.1	1.25
27	154.2	122.0	1.26
41	164.7	133.6	1.23
30	175.0	142.0	1.23
22	185.5	148.8	1.25
12	193.3	153.4	1.26
12	204.1	170.4	1.20
8	213.2	180.2	1.18
3	222.3	181.3	1.23
3	233.7	198.3	1.18
1	265.0	198.0	1.34

⁴Details concerning the exact location of the key scales and methods of measurement are given by Jobes (MS.).

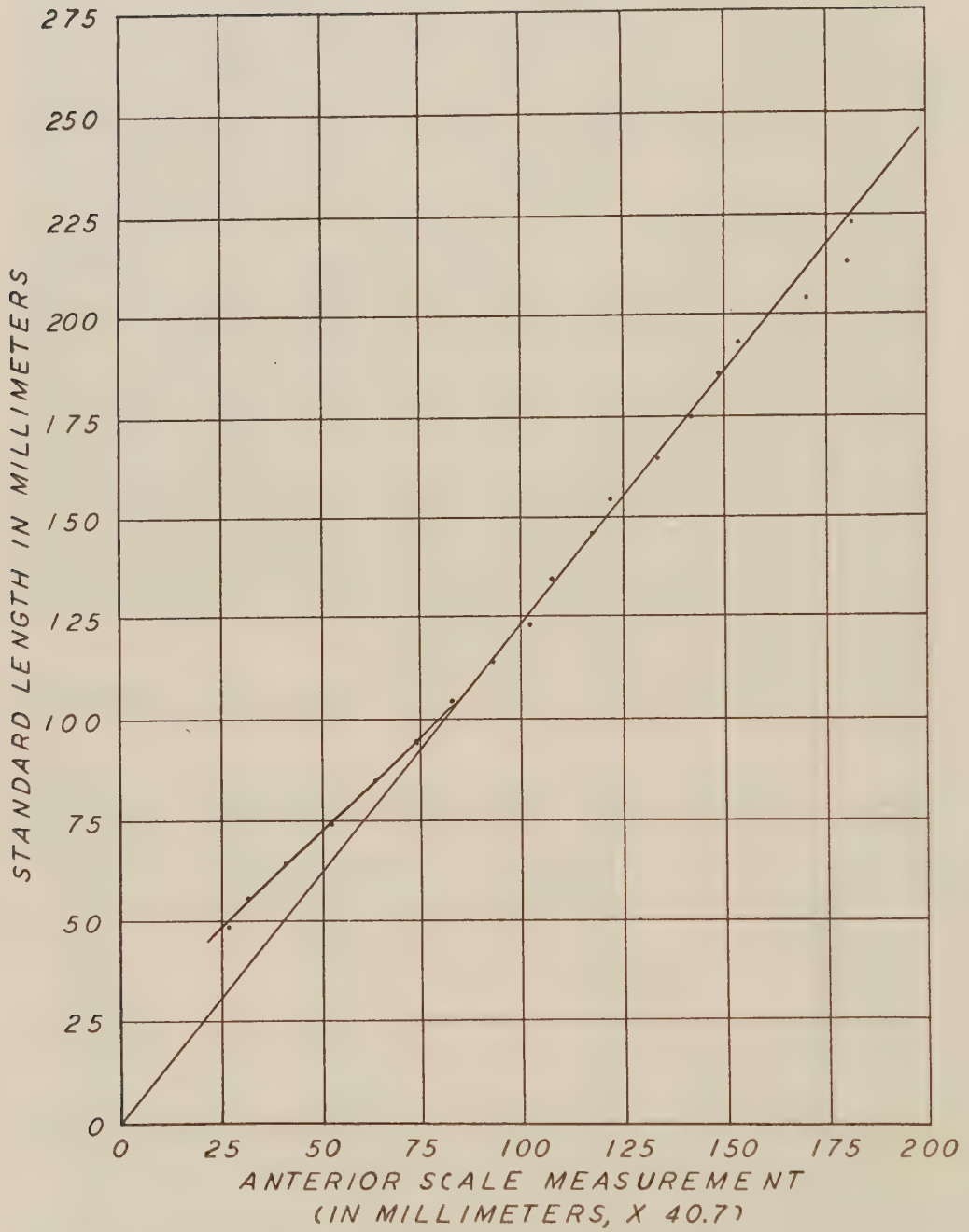


Figure 2.—Relationship between the standard length of Saginaw Bay yellow perch and the measurements of (magnified) key scales

becomes constant. Calculated lengths below that point must be corrected to compensate for the disproportionate growth of body and scale. Although these corrections can be read directly from the curve, it has been found more convenient to prepare Table 5 which lists the "correction" to be added to each direct-proportion calculated length.⁵ The table contains corrections for direct-proportion calculated lengths as high as 101 millimeters, although a constant body-scale ratio was assumed for all lengths beyond 90 millimeters. The necessity for corrections of lengths over the interval, 90-101 millimeters, arises from the fact that the natural continuation of the body-scale curve that was drawn free-hand for the smaller fish meets the line, $L = 1.24 Sc$, at the length of approximately 103 millimeters rather than at 90 millimeters. The corrections in the interval, 90-101 millimeters, do not exceed 3 millimeters and are only 1 or 2 millimeters at most lengths.

All first-year calculated lengths fell within the range for which a correction was necessary. Part of the calculated lengths for the second year but none for later years needed to be corrected.

Table 5.—Correction (in millimeters) to be added to direct-proportion calculated lengths to compensate for the disproportionate growth of body and scale in small Saginaw Bay yellow perch

Interval of direct-proportion calculated length (millimeters)	"Correction" to be added (millimeters)	Interval of direct-proportion calculated length (millimeters)	"Correction" to be added (millimeters)
38-40	16	68-72	8
41-45	15	73-75	7
46-49	14	76-79	6
50-53	13	80-83	5
54-58	12	84-88	4
59-60	11	89-91	3
61-64	10	92-95	2
65-67	9	96-101	1

AGE COMPOSITION AND LENGTH FREQUENCIES

The age composition of each year's sample and of the combined collections of Saginaw Bay yellow perch is given in Table 6. The 1929 collection was characterized by the strong dominance of age-group IV (72.0 per cent of the entire sample). Age-group III was dominant in 1930 (49.4 per cent) but age-group IV was more than half as strong (25.1 per cent) and age-group V also was well represented (19.3 per cent). In the combined collections age-groups III and IV were almost exactly of equal abundance. Of the remaining four age groups only the V group contained a large number of fish. The scarcity of II-group perch in the collections is traceable in part to the selective action of the gear, whose meshes were too large to retain the smaller perch.

⁵Jobs (MS.) gave a discussion of the use of the empirical body-scale curve for the determination of corrected calculated lengths and explained the procedure by which a table of the type of Table 5 is prepared.

Biological segregation according to maturity also may have contributed to the scarcity of perch of the younger age groups. The samples were taken almost exclusively from the spawning run which includes only the mature (older) perch. However, the small numbers of perch of age-groups VI and VII reflect a scarcity of older fish on the fishing grounds.

Although the data of Table 6 are not adequate for a detailed analysis of the relative strengths of the year classes represented, it does appear valid to conclude that the 1925 year class was one of greater than average strength. The chief argument for this conclusion lies in the strong dominance of the 1925 year class as the 1929 IV group. In this year's sample age-group IV was 5.7 times as abundant as age-group III and 6.6 times as abundant as age-group V. The same year

Table 6.—*Age and year-class composition of collections of yellow perch from Saginaw Bay*

Year of capture	Item	Age group					
		II	III	IV	V	VI	VII
1929	Number of fish	7	30	172	26	2	2
	Percentage of sample..	2.9	12.6	72.0	10.9	0.8	0.8
	Year class	1927	1926	1925	1924	1923	1922
1930	Number of fish	18	287	146	112	15	3
	Percentage of sample..	3.1	49.4	25.1	19.3	2.6	0.5
	Year class	1928	1927	1926	1925	1924	1923
1929 and 1930	Number of fish	25	317	318	138	17	5
	Percentage of sample..	3.0	38.7	38.8	16.8	2.1	0.6

class, as the 1930 V-group, was only slightly less abundant than fish a year younger. As a possible alternate explanation of the great abundance of the 1925 year class in the collections it might be held that the 1926 year class was exceptionally weak. With either interpretation the data for Saginaw Bay provide a striking contrast with Lake Erie, where 1926 saw the production of a phenomenally rich year class not only of yellow perch but of several other species as well (Van Oosten, 1938).

Preliminary tabulations failed to reveal significant differences in the length-frequency distributions of perch of the same age and sex in the two years' collections. Accordingly the length frequencies of Table 7 have been based on a combination of the 1929 and 1930 data. It may be seen readily that the extensive overlap of the frequency distributions of the successive age groups makes the length of an individual a relatively poor index of its age. Over intervals in which fish are abundant an individual fish of a particular length may belong to any one of two or three (usually three) age groups. The length-frequency distributions are characterized further by the tendency for the modal lengths of the females to be greater than those of males of corresponding age. This situation is reflected in the higher average

Table 7.—Length-frequency distribution of Saginaw Bay yellow perch according to age and sex. The 1929 and 1930 collections have been combined. The legal length of 187 millimeters corresponds to the total length of $8\frac{1}{2}$ inches

Standard length interval (millimete.s)	II		III		IV		V		VI		VII		II-VII		Total ³
	M ¹	F ²	M	F	M	F	M	F	M	F	M	F	M	F	
120-124	1	..	..	..	..	..	..	..	..	..	..	..	1	..	3
125-129	3	..	..	..	..	..	..	..	..	..	..	..	3	..	3
130-134	2	..	..	..	..	..	..	..	..	..	..	..	2	..	2
135-139	..	1	..	..	..	..	..	..	..	..	..	..	..	1	2
140-144	..	1	2	..	..	..	..	..	..	..	..	..	2	1	5
145-149	2	3	..	1	..	..	..	..	..	..	..	..	2	4	7
150-154	..	..	..	..	..	..	..	..	..	..	..	..	2	..	2
155-159	..	1	2	2	2	..	..	..	..	..	..	..	5	..	10
160-164	..	2	3	8	..	..	..	..	..	..	..	..	3	10	19
165-169	1	..	7	5	1	..	..	..	..	..	..	..	8	18	26
170-174	..	3	11	17	1	..	..	..	..	..	..	..	13	5	24
175-179	..	..	4	22	1	2	..	..	..	..	..	..	5	20	32
180-184	..	..	7	28	3	3	..	..	..	..	..	..	8	31	44
185-189	..	..	10	43	5	3	..	..	..	..	..	..	13	46	58
190-194	..	..	7	38	11	7	1	1	..	..	..	..	15	46	61
195-199	..	..	3	21	11	11	1	1	..	..	..	..	13	33	46
200-204	..	..	1	19	8	26	1	..	..	..	..	..	9	45	56
205-209	..	..	..	12	4	17	1	..	..	..	..	..	8	33	46
210-214	..	..	..	12	13	27	2	3	..	..	..	..	15	42	57
215-219	..	..	..	12	7	26	1	6	..	..	..	..	8	44	52
220-224	..	..	2	5	6	27	10	6	..	..	..	..	9	38	47
225-229	..	..	..	..	3	29	18	6	..	..	..	..	13	35	48
230-234	..	..	..	..	4	20	2	13	..	1	..	..	12	34	48
235-239	..	..	..	1	5	11	3	10	..	2	..	..	7	20	27
240-244	..	..	..	..	1	12	4	7	..	..	..	..	4	24	29
245-249	..	..	..	..	..	6	4	7	..	3	..	..	4	13	17
250-254	..	..	..	..	..	1	2	13	1	..	..	..	3	17	20
255-259	..	..	..	..	..	1	1	6	1	4	..	..	2	7	9
260-264	..	..	..	..	..	..	1	6	1	..	..	..	1	11	12
265-269	..	..	..	..	..	..	..	2	1	..	..	..	..	3	4
270-274	..	..	..	..	..	..	..	2	2	..	..	..	..	2	2
275-279	..	..	..	..	..	..	..	2	2	3	..	..	..	6	6
280-284	..	..	..	..	..	..	1	1	..	..	..	..	2	1	3
285-289	..	..	..	..	..	..	..	1	..	..	..	..	..	1	2
Number of fish.....	9	11	62	246	87	229	39	98	4	13	2	3	203	600	820
Average standard length.....	136	156	176	191	205	218	232	240	250	258	284	269	200	211	207
Percentage illegal (less than 187 millimeters)	100.0	100.0	83.9	46.3	13.8	2.6	0.0	0.0	0.0	0.0	0.0	0.0	36.0	21.8	26.1

¹M—Male.²F—Female.³Includes 17 fish for which sex records were lacking.

lengths of the females in all age groups but the poorly represented VII group.

The percentage of illegal-sized perch (less than 8½ inches, total length) in each age group has been given at the bottom of Table 7. All II-group perch were undersized near the beginning of the third year of life. However, the presence of legal-sized fish in age-group III suggests the possibility that a few II-group yellow perch may attain legal size during the third growing season. Most of the III-group males (83.9 per cent) were below legal length but only 46.3 per cent of the females fell below 8½ inches. Continued growth during the fourth year of life doubtless brings about a large increase in the percentage of legal-sized fish in age-group III. This belief is supported by the observation that a high percentage of IV-group perch was above legal length at the beginning of the fifth growing season. No undersized perch occurred in age-groups V, VI, or VII. The percentages of undersized perch for all age groups combined were 36.0 per cent for the males, 21.8 per cent for the females, and 26.1 per cent for the sexes combined.

The data on the age composition and the length distribution of the yellow perch of the samples from Saginaw Bay reveal that the commercial fishery is supported almost entirely by age-groups III, IV, and V. The inclusion of age-group III is justified by the fact that the bulk of the commercial catch is produced in late season at which time III-group fish have completed most or all of their fourth-year growth. The four months, September to December, accounted for 77 per cent of the total 1936-1938 production of perch. The percentage was 45 for October alone.

GROWTH IN LENGTH AND WEIGHT

The length and weight at capture and the calculated growth history of each age group in each year's collection of Saginaw Bay yellow perch are given for the males in Table 8 and for the females in Table 9. A separation of data has been made also according to year class. At the bottoms of the tables may be found the grand average lengths at the end of each year of life and the growth increments during each year of life. The data for the II groups were not employed in the computation of the grand averages. The small numerical representation of yellow perch of this age together with their high calculated lengths (particularly in the 1930 samples) suggested that the gear employed for the collection of the samples may have taken only the larger II-group fish. Gear selection may have affected somewhat the reliability of the III groups also; however, the extremely strong representation of this age group in the 1930 collection indicates that the selection was not very severe. Consequently the data for all III groups were employed in the calculation of grand averages.

Most of the discrepancies between corresponding calculated lengths of different age groups of males can be attributed to the small num-

Table 8.—Average length and weight at capture of male yellow perch from Saginaw Bay and the average calculated length attained by the age groups (and year classes) at the end of each year of life

Year class	Year of capture	Age group	Number of fish	Weight (ounces)	Total length (inches)	Weight (grams)	Standard length (mm.)	Calculated standard length in millimeters at end of year						
								1	2	3	4	5	6	7
1922	1929	VII	2	12.75	12.8	361	284	62	114	160	209	246	268	284
1924	1929	V	4	8.12	10.7	230	235	64	104	156	204	235	250	..
1925	1930	VI	4	11.19	11.2	317	250	69	104	138	178	220	250	..
1925	1929	IV	46	5.39	9.2	153	203	62	106	161	202	232	..	..
1926	1930	V	35	8.30	10.6	235	232	63	104	161	205	232	..	..
1926	1929	III	6	4.47	8.8	127	194	70	136	192	207	..	..	..
1927	1930	IV	41	6.04	9.5	171	208	68	118	169	..	..	..	..
1927	1929	II	2	1.20	5.8	34	126	69	126	..	..	..	..	..
1930	1930	III	56	3.25	8.1	92	174	65	123	172	..	..	..	..
1928	1930	II	7	1.79	6.4	51	139	84	139	..	..	..	..	..
Grand average calculated length ²								65	114	166	204	232	259	275
Grand average calculated increment of length ³								65	49	52	38	28	27	16

¹Age group not employed in the computation of grand averages.

²Grand average calculated lengths at the end of the sixth and seventh years of life were obtained by the successive addition of the grand average increments of growth in the sixth and seventh years to the grand average calculated length at the end of the fifth year.

Table 9.—Average length and weight at capture of female yellow perch from Saginaw Bay and the average calculated length attained by the age groups (and year classes) at the end of each year of life

Year class	Year of capture	Age group	Number of fish	Weight (ounces)	Total length (inches)	Weight (grams)	Standard length (mm.)	Calculated standard length in millimeter at end of year						
								1	2	3	4	5	6	7
1923	1929	VI	2	10.50	11.1	298	247	64	103	143	188	220	242	..
1930	1930	VII	3	12.83	12.1	364	269	63	101	141	179	216	246	269
1929	1929	V	21	8.45	10.6	240	234	65	109	153	193	232	..	..
1930	1930	VI	11	11.48	11.7	325	260	60	96	140	180	222	260	..
1925	1929	IV	124	7.12	10.0	202	219	64	108	166	218	..	..	..
1930	1930	V	77	9.27	10.8	263	241	62	105	160	208	241	..	..
1926	1929	III	15	4.10	8.4	116	185	67	119	182	..	..	..	..
1929	1930	IV	105	6.27	9.9	178	217	65	114	171	214	..	..	..
1930	1930	III	231	4.23	8.7	120	191	66	126	187	..	..	..	..
1927	1930	II	11	2.43	7.2	69	156	82	153	..	..	..	..	..
1928	1930	II	11	2.43	7.2	69	156	82	153	..	..	..	..	..
Grand average calculated length ³								65	116	174	211	236	270	293
Grand average calculated increment of length ³								65	51	58	37	25	34	23

¹The average weight is based on one less fish than employed to obtain the average lengths.

²Age group not employed in the computation of grand average.

³Grand average calculated lengths at the end of the sixth and seventh years of life were obtained by the successive addition of the grand average increments of growth in the sixth and seventh years to the grand average calculated length at the end of the fifth year.

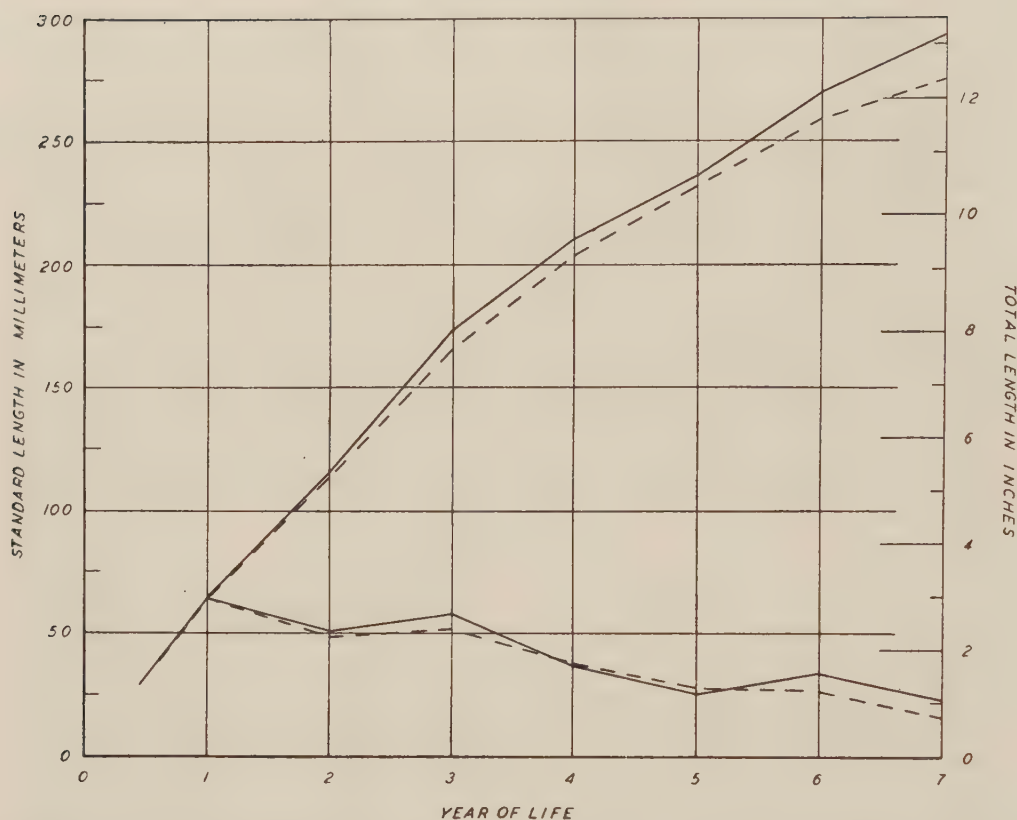


Figure 3.—Calculated lengths at the end of each year of life (upper curves) and increments of growth in length in each year of life (lower curves) of Saginaw Bay yellow perch, males — — —, females — — —.

bers of specimens in the different age groups. There was almost perfect agreement between the growth histories of the two age groups of the only year class (year class of 1925) that was well represented in both years' collections. The data for the females, on the other hand, appear to contain discrepancies in calculated growth histories, correlated with age. The younger age groups of the 1924, 1925, and 1926 year classes consistently had higher calculated lengths than older fish of the same year class. A complete discussion of possible factors contributing to this type of discrepancies in calculated growth was presented by Jobes (MS.) and hence need not be included here. It should be pointed out, nevertheless, that errors originating in the method of calculating growth do not seem to be a factor.

The general growth curves of both sexes contain inflections. (See Fig. 3.) The greatest growth in length occurred in the first year of life. Growth declined in the second year but improved in the third. Beyond the third year the annual increments of length of the males decreased continually. The growth increments of the females decreased from the third to the sixth year of life, increased in the sixth

year and decreased again in the seventh year. It is unlikely that the increase in the growth increment that occurred in the sixth year of life is typical for females of the Saginaw Bay yellow perch.

The legal length of $8\frac{1}{2}$ inches, total length (187 millimeters, standard length), falls between the third-year and fourth-year calculated lengths of both sexes. On the average, females attained the legal length earlier in the fourth growing season than did the males.

Table 10 contains data on general growth in weight, that correspond exactly to the general curves of growth in length; that is, the weight corresponding to each grand average calculated length has been computed from the length-weight equation given on page 118. The resulting curves of growth in weight (both in grams and ounces) are presented in Figure 4. The positions of the average weights of the age groups at capture, with the data for corresponding age groups of the two years' collections combined, are shown by small triangles for the males and dots for the females. It may be seen that the empirical averages of the age groups of both sexes fall rather closely along their

Table 10.—Calculated weights in grams corresponding to the grand average calculated lengths of Saginaw Bay yellow perch at the end of each year of life, and the annual increments of growth in weight

Sex	Item	Year of life						
		1	2	3	4	5	6	7
Male	Calculated weight	4	25	82	156	233	328	395
	Increment of weight.....	4	21	57	74	77	95	67
Female	Calculated weight	4	27	95	173	245	373	482
	Increment of weight.....	4	23	68	78	72	128	109

respective theoretical curves. Since the average length of VII-group males at capture exceeded the calculated length at the end of the seventh year the weight of this age group at capture cannot be shown in Figure 4.

The annual increments of growth in weight of males increased continuously during the first 6 years of life and decreased in the seventh. The increase in the annual increments of weight of females was interrupted by a small decline in the fifth year. The growth of the females improved notably in the sixth year but fell away in the seventh. The Saginaw Bay yellow perch becomes subject to capture in the commercial fishery just as it is entering on the period of most rapid growth in weight. In fact, the greatest growth in weight of both sexes occurred in the sixth year of life, approximately two years subsequent to the attainment of legal length.

RELATIONSHIP BETWEEN TOTAL LENGTH AND STANDARD LENGTH

Since many scientific papers list only standard lengths, whereas anglers and conservationists employ total lengths, a knowledge of the relationship between the two measurements is of practical value.

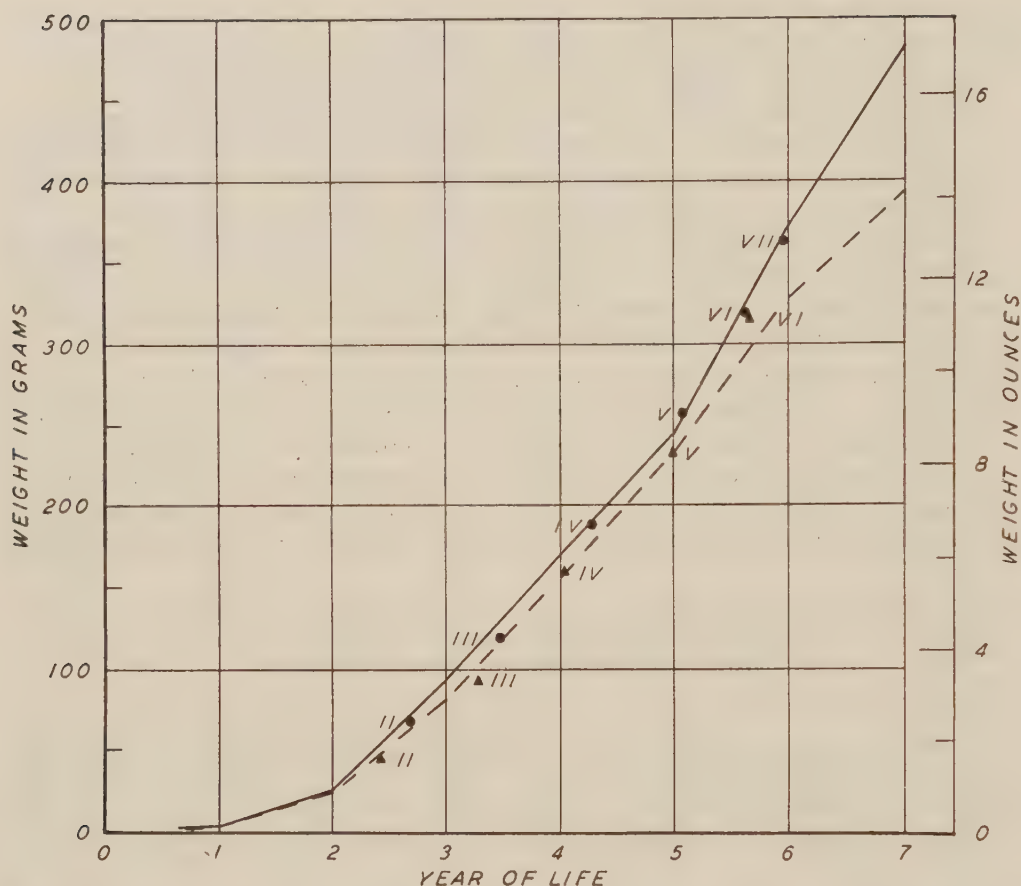


Figure 4.—Calculated growth in weight of Saginaw Bay yellow perch, males ———, females ————. The weights of the age groups at capture are shown by small triangles for the males and dots for the females.

Table 11 contains the factors for conversions between total length and standard length, both with and without change of units of measurement. These factors vary according to the size of the fish, since the relative length of the tail tends to decrease with increase in the length of the fish. A similar change in the relative size of the caudal fin was observed by Van Oosten (1938) for the Lake Erie sheepshead and for the Lake Huron whitefish (Van Oosten, 1939). Preliminary compilations revealed a tendency for the tails of female yellow perch to be relatively shorter than those of males. This sex difference was not sufficiently great, however, to make necessary the determination of conversion factors for the sexes separately.

LENGTH-WEIGHT RELATIONSHIP AND CONDITION

The data on the length-weight relationship of the Saginaw Bay perch (Table 12, Fig. 5) have been based on 1,483 fish captured in the

Table 11.—Factors for the conversion of total (T. L.) and standard (S. L.) lengths of the Saginaw Bay yellow perch

Standard length (millimeters)	Number of fish	Conversion factors			
		T.L. to S.L. (No change of unit)	S.L. to T.L. (No change of unit)	S.L. (millimeters) to T.L. (inches)	T.L. (inches) to S.L. (millimeters)
Under 175.....	248	0.849	1.177	0.0464	21.57
175—239	996	0.866	1.155	0.0455	22.00
Over 239	167	0.877	1.141	0.0449	22.27

autumn of 1928, the spring and autumn of 1929, and the springs of 1930 and 1934. Figure 5 has been so arranged as to permit ready conversions from standard lengths in millimeters and weights in grams to total lengths in inches and weights in ounces.

The dots in Figure 5 represent the empirical averages of length and weight; the smooth curve is the graph of the equation,

$$W = 0.9826 \times 10^{-5} L^{3.1174},$$

which was derived by fitting a straight line to the logarithms of the average lengths and weights⁶ in the length interval, 140-264 millimeters. In the logarithmic form the equation may be expressed as,

$$\log W = -5.00754425 + 3.1174 \log L.$$

In both equations W = weight in grams and L = length in millimeters. The value of the exponent, 3.1174, shows that the weight of Saginaw Bay yellow perch increases somewhat more rapidly than the cube of the length.

Table 12.—Relationship between the length and the weight of Saginaw Bay yellow perch. (See text for method of determining the calculated weights.)

Number of fish	Standard length (millimeters)	Weight (grams)		Total length (inches)	Weight (ounces)
		Empirical	Calculated		
8	125	32	34	5.8	1.1
19	135	42	43	6.3	1.5
35	145	52	54	6.7	1.8
48	154	68	65	7.1	2.4
96	165	82	80	7.7	2.9
104	175	97	97	8.0	3.4
169	185	111	115	8.4	3.9
198	194	134	133	8.8	4.7
188	204	155	156	9.3	5.5
178	214	186	181	9.7	6.6
162	224	215	208	10.2	7.6
111	233	235	236	10.6	8.3
69	244	269	272	11.0	9.5
41	253	300	305	11.4	10.6
29	263	351	344	11.8	12.4
13	275	360	395	12.3	12.7
10	285	402	442	12.8	14.2
1	295	502	492	13.2	17.7
1	338	462	752	15.2	16.3
3	351	508	846	15.8	17.9

⁶Originally the average lengths and weights were determined by 5-millimeter rather than centimeter length intervals, and it was from these 5-millimeter averages that the constants for the equation were determined.

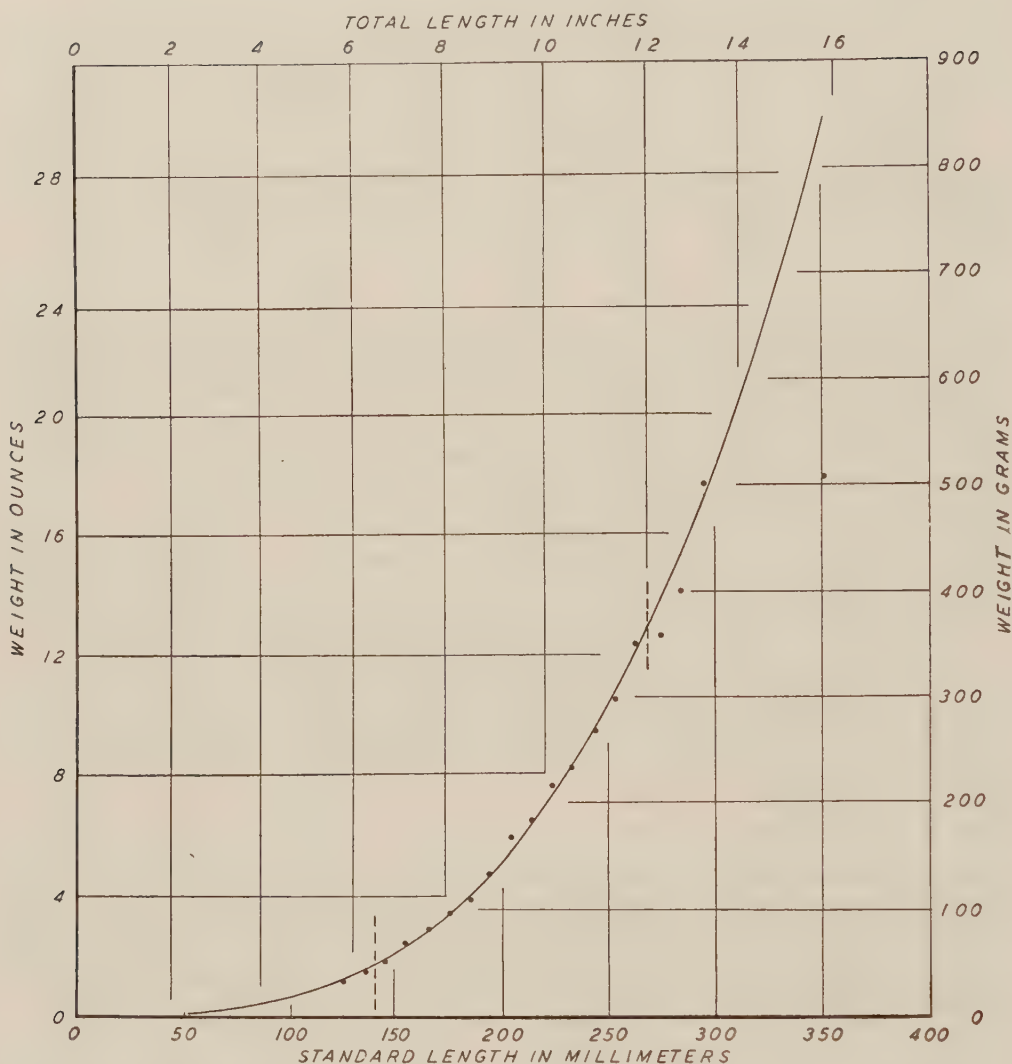


Figure 5.—Length-weight relationship of the Saginaw Bay yellow perch (sexes combined). The broken vertical lines indicate the limits of the length range over which the length-weight equation was fitted.

Comparisons of the empirical weights with those calculated from the length-weight equation (Table 12) reveal good agreement over the length interval for which the equation was fitted. The greatest discrepancy was only 7 grams (at 224 and 263 millimeters) and the mean of the absolute values of the discrepancies was only 3.2 grams. The agreement between calculated and empirical weights was close also at 125 and 135 millimeters. At the greater lengths (beyond 263 millimeters) the calculated and empirical weights disagreed radically. To some extent these discrepancies may depend on the small number of specimens. The data provide some evidence, however, that old

Table 13.—Average coefficient of condition (K) for the age groups of Saginaw Bay yellow perch. The sexes are combined

Number of fish	Age group	K
25	II	1.75
317	III	1.72
317	IV	1.83
137	V	1.84
17	VI	1.92
5	VII	1.74

perch may tend to be lighter than would be expected on the assumed theoretical grounds.

The Saginaw Bay yellow perch weighs approximately 4 ounces when it attains the legal length of 8½ inches.

The coefficient of condition⁷, K , was computed for every fish whose age was determined. (Weights were lacking for 2 of the 820 specimens.) The variation of condition with age is indicated in Table 13.

The grand average coefficient of condition was 1.79 for each sex. This value indicates that the Saginaw Bay yellow perch has a more slender body form than the Lake Erie yellow perch. The average K for the perch in Lake Erie was found to be 1.91 (Jobes, MS.).

Table 14.—Number of males and females in each age group of Saginaw Bay yellow perch, and the sex ratio expressed as number of females per 100 males

Age group	Number of males	Number of females	Females per 100 males
II	9	11	122
III	62	246	397
IV	87	229	263
V	39	98	251
VI	4	13	325
VII	2	3	150
II-VII	203	600	296

MATURITY AND SEX RATIO

Of the 820 perch whose ages were determined, 788 or 96 per cent were mature. A high percentage of mature individuals is to be expected in collections that are composed chiefly of spawning-run samples.

Sex data were available for 803 specimens. The distribution of the sexes according to age (1929 and 1930 collections combined) may be seen in Table 14.

Females predominated in every age group. For all age groups combined the females outnumbered the males in the ratio, 296:100. The variations of the sex ratio among the age groups failed to exhibit a distinct trend.

It should be mentioned that data on the sex ratio obtained from spawning-run collections may not be descriptive of the true sex ratio of the general population. Commonly the sex ratio shifts during the spawning season from a predominance of males near the beginning of the period to a predominance of females toward the close. Consequent-

⁷ $K = \frac{W \times 10^5}{L^3}$, where W = weight in grams and L = length in millimeters.

ly the sex ratios of spawning-run samples vary according to the time of collection in the spawning season. The great relative abundance of females in the perch collections from Saginaw Bay lends support to the belief that females may predominate in the population toward the close of the spawning run since most of the samples were taken late in the spawning season. (Only a few samples were collected subsequent to the spawning period.)

SUMMARY

1. Although the yellow perch grounds of Saginaw Bay continue to be the most productive in the State of Michigan waters of the Great Lakes, the average annual yield over the period, 1917-1938, has been only 28 per cent of the earlier (1891-1916) normal.

2. The shallow trap net accounts for the bulk of the catch of Saginaw Bay yellow perch in the modern fishery (71.5 per cent of the 1929-1938 production).

3. Detailed statistical analyses for the 10 years, 1929-1938, revealed that production, the abundance of perch on the grounds, and the intensity of the fishery for perch are subject to large annual fluctuations. The maximum annual production of the period was roughly three times the minimum. The maxima of abundance and fishing intensity were about twice the minima.

4. The study of the growth of the Saginaw Bay yellow perch was based on the determination of the age and the calculation of growth from the examination and measurement of the scales of 820 individuals captured in pound nets in the spring and early summer fishing seasons of 1929 and 1930. The numbers of specimens employed in other phases of the study were: Body-scale relationship—512 fish captured at various dates from April to November in the years, 1921, 1925-1927, 1930, and 1934; relationship between total length and standard length—1,411 perch collected in 1928-1930 and 1934; length-weight relationship—1,483 individuals taken in 1928-1930 and 1934.

5. The constancy of the body-scale ratio among the larger perch makes the use of the direct-proportion method of calculating individual growth histories valid at all calculated lengths above 101 millimeters. Calculated lengths of 101 millimeters or less were corrected (from an empirical curve of the body-scale relationship) to compensate for the disproportionate growth of body and scale in small fish.

6. The modal lengths of the length-frequency distributions of females tended to be greater than those of males of corresponding age. The length frequencies of the successive age groups of both sexes exhibited extensive overlap. In the complete sample (age groups and sexes combined) 26.1 per cent were below the legal length of 8½ inches.

7. The 1929 collection was dominated by the 1925 year class as age-group IV (72.0 per cent of the total) and the 1930 collection was dominated by the 1927 year class as age-group III (49.4 per cent). Age-group III and IV were equally represented in the combined 1929-1930

collections (approximately 39 per cent each). The 1925 year class appears to have been unusually strong.

8. Females grew more rapidly than did the males. The greatest growth in length of both sexes occurred in the first year of life. The annual growth increments decreased in the second year and increased in the third. Beyond the third year of life the annual length increments decreased continuously for the males and irregularly for the females. Both sexes attained the legal length of 8½ inches during the fourth year of life.

9. The greatest annual increment of weight of both sexes occurred in the sixth year of life. The annual increments of growth in weight increased continuously during the first 6 years of life of the males and during the first 4 years of life of the females. The Saginaw Bay yellow perch becomes subject to capture in the commercial fishery just as it is entering the period of most rapid growth in weight.

10. The ratio of standard length to total length increased with increase in the length of the fish.

11. Over the length interval, 120-265 millimeters, the length-weight relationship was described satisfactorily by the equation,

$$W = 0.9826 \times 10^{-5} L^{3.1174},$$

where W = weight in grams and L = length in millimeters. At most lengths greater than 265 millimeters the actual weights were smaller than those computed from the equation.

12. The average value of the coefficient of condition, K , of the age groups varied from 1.72 to 1.92. For all age groups combined the average K was 1.79.

13. Ninety-six per cent of the yellow perch whose ages were determined were mature. Females outnumbered the males in the ratio, 296:100, and were in the majority in every age group.

LITERATURE CITED

Harkness, W. J. K.

1922. The rate of growth of the yellow perch (*Perca flavescens*) in Lake Erie. Univ. Toronto Studies, Pub. Ont. Fish. Res. Lab., No. 6, pp. 89-95, 2 figs.

Hile, Ralph

1937. The increase in the abundance of the yellow pike-perch, *Stizostedion vitreum* (Mitchill), in Lakes Huron and Michigan, in relation to the artificial propagation of the species. Trans. Am. Fish. Soc., Vol. 66 (1936), pp. 143-159, 5 figs.

Jobes, Frank W.

1933. Preliminary report on the age and growth of the yellow perch (*Perca flavescens* Mitchill) from Lake Erie, as determined from a study of its scales. Pap. Mich. Acad. Sci., Arts, Let., Vol. 17 (1932), pp. 643-652, 3 figs.

Van Oosten, John

1938. The age and growth of the Lake Erie sheepshead, *Aplodinotus grunniens* Rafinesque. Pap. Mich. Acad. Sci., Arts, Let., Vol. 23 (1937), pp. 651-668, 3 figs.
1939. The age, growth, sexual maturity, and sex ratio of the common whitefish, *Coregonus clupeaformis* (Mitchill), of Lake Huron. *Ibid.*, Vol. 24, Part II (1938), pp. 195-221, 3 figs.

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BATHYMETRIC DISTRIBUTION OF FISH IN LAKES OF THE NORTHEASTERN HIGHLANDS, WISCONSIN¹

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INTRODUCTION

The present study of the bathymetric distribution of fish in the lakes of northeastern Wisconsin has been based on records of the catches of gill nets fished during the summers of 1930, 1931 and 1932. During the first of the three summers, soundings were made only of the general area in which each gang of nets was fished. In 1931 and 1932, however, individual records were made of the depths from which almost all of the nets were lifted. The more exact data obtained in these two years form the basis for most of the material that will be presented, although some references will be made to the fishing operations of 1930.

The limnological data of Table 1 indicate the general nature of the five lakes, the distribution of whose fish populations will be described. The location of four of the lakes (Nebish, Muskellunge, Trout and Silver) may be seen in Figure 1. Clear Lake lies about 13 kilometers (8 miles) southeast of Trout Lake. Trout Lake is the second largest and the deepest lake of the Northeastern highlands. In comparison with other Lakes of the region its waters are relatively hard. Muskellunge Lake and Clear Lake are of intermediate and similar size. Clear Lake has very soft water, particularly for a lake so large, whereas the water

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of Muskellunge Lake may be termed medium hard. Silver Lake and Nebish Lake are both small. They differ, however, as to the hardness of their waters; the concentration of bound CO_2 is 15.0 p. p. m. in Silver Lake as compared to 4.0 p. p. m. in Nebish Lake. Limnological data concerning all of these lakes have appeared from time to time in publications of the Wisconsin Geological and Natural History Survey.

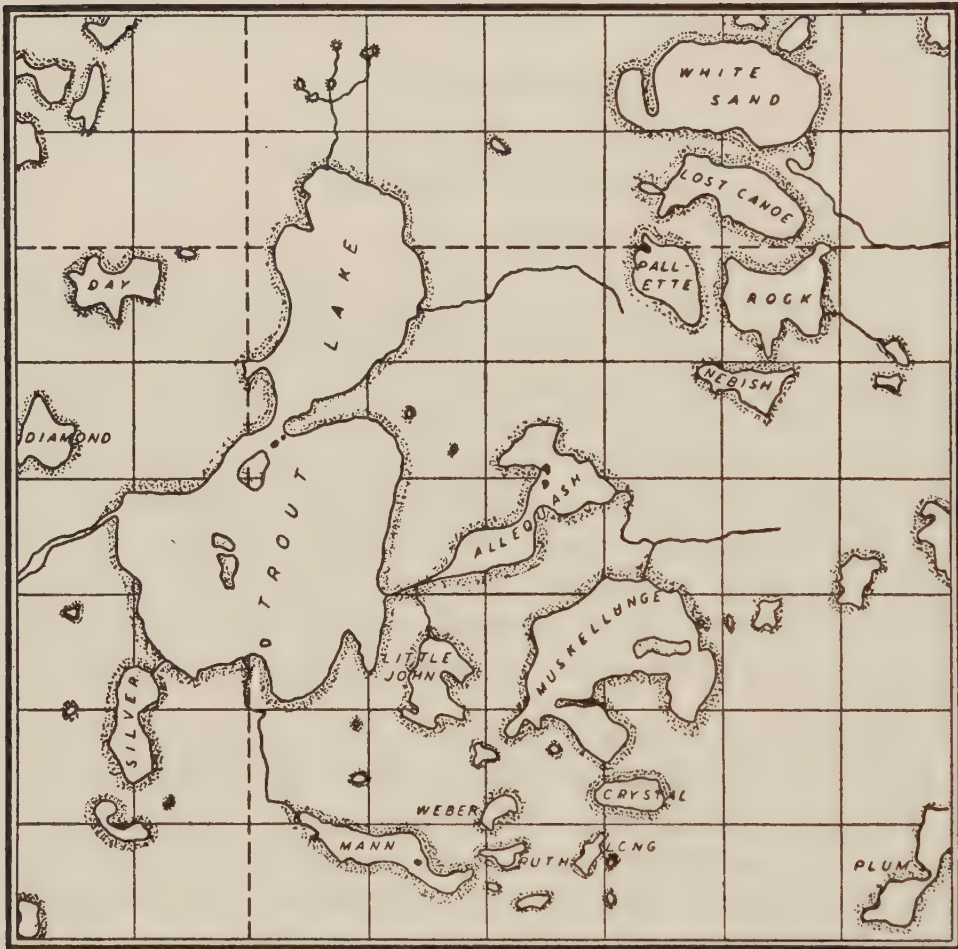


FIG. 1. Map of Trout Lake region.

TABLE 1. Limnological data on five Lakes of the northeastern highlands, Wisconsin. The data for color, pH, conductivity, bound CO₂, and the organic matter of the plankton refer to average surface conditions in summer.

Lake	Length in kilometers	Breadth in kilometers	Surface area (hectares)	Length of shore line in kilometers	Depth in meters	
					Maximum	Mean
Nebish	1.32	0.66	38.5	4.2	15.8	5.2
Muskellunge	3.12	2.00	372.3	14.5	21.0	7.0
Trout North basin	7.00	4.00	533	25.9	31.0	12.9
Trout South basin	1.75	0.66	1,050	4.3	35.0	14.2
Silver	3.36	2.04	87.3	22.2	19.5	11.3
Clear			417.8		29.3	8.8
Lake	Secchi disc transparency (meters)	Color, platinum-cobalt scale	pH	Conductivity in reciprocal megohms	Bound CO ₂ in milligrams per liter	Organic matter of plankton in milligrams per liter
Nebish	6.0	9	6.8	19	4.0	0.77
Muskellunge	4.0	4	7.2	40	10.0	1.16
Trout North basin	5.0	6	7.8	73	18.5	0.66
Trout South basin	4.5	3	7.6	77	18.7	0.92
Silver	5.5	4	7.5	62	15.0	0.85
Clear	6.3	0	6.6	17	2.2	0.84

METHODS

The gill nets fished in 1930 and the early summer of 1931 included the following sizes of mesh (stretched measure in inches): $1\frac{1}{2}$, 2, $2\frac{1}{2}$ and $3\frac{1}{4}$. The depth of these nets ranged from $3\frac{1}{2}$ to 4 feet. A complete replacement of gear was made July 22, 1931. The new nets included seven sizes of mesh (stretched measure in inches): $1\frac{1}{4}$, $1\frac{1}{2}$, $1\frac{3}{4}$, 2, $2\frac{1}{4}$, $2\frac{1}{2}$ and 3. Each of these nets was 50 yards long and approximately 6 feet deep. Thus the area of each net was roughly 100 square yards. All tabular material on the average catch per lift has been based on data from the "new" nets.

Ordinarily the gill nets were fished in gangs of seven nets, and were lifted daily. The different sizes of mesh were not arranged in a gang in any definite order. The sets were made along rather than across the contours of the lake since this procedure made possible a more accurate determination of the depth at which each net was set. The mean of the soundings at the ends of each net has been taken as the depth from which the net was lifted.

At the time the nets were lifted the catches from the different meshes were placed separately in labeled pails. Counts and measurements of the fish from each net were made later at the field laboratory.

The description of the bathymetric distribution of fish will include a consideration of the relationship between the length of fish and the depth of water inhabited. Since the data on which the discussion will be based will consist of records of the average numbers of fish captured in different sizes of mesh at the various depths of water, a knowledge of the relationship between the size of mesh and the average length of the fish captured is of considerable importance. Table 2 shows the relationship between the size of gill-net meshes and the average length of the fish taken for each species of each lake for which detailed tabular material will be presented in later sections². It is apparent that the relationship between length of fish and size of mesh is sufficiently close to make valid the use of the numbers of fish captured in different sizes of mesh for the study of the bathymetric

² The data of Table 2 relative to the perch of Nebish and Silver lakes were computed from tabulations given by Schneberger (1935). The remaining data were compiled originally for this report.

distribution of fish of different size. In other words, if small-mesh nets made their best catches in shallow water and large-mesh nets fished most successfully in deep water it may be concluded that the smaller fish were living in shallower water than were the larger individuals.

TABLE 2. Average standard length in millimeters of fish taken by gill nets of different mesh size in four lakes of northeastern Wisconsin. Numbers of specimens in parentheses.

Lake	Species	Average length of fish taken in mesh (stretched measure)						
		1¼ inches	1½ inches	1¾ inches	2 inches	2¼ inches	2½ inches	3 inches
Nebish	Rock bass	86 (17)	92 (172)	116 (79)	134 (92)	156 (70)	162 (224)	177 (350)
	Perch	122 (35)	144 (115)	166 (120)	182 (48)	202 (9)	222 (3)	
	Smallmouth black bass	113 (38)	130 (23)	169 (12)	177 (25)	199 (22)	215 (14)	249 (10)
Muskellunge	Rock bass	83 (97)	92 (79)	121 (40)	142 (50)	149 (66)	158 (71)	175 (37)
	Perch	115 (493)	140 (95)	168 (39)	175 (51)	198 (51)	211 (36)	164 (7)
	Common sucker	133 (30)	143 (119)	169 (114)	196 (152)	221 (283)	236 (384)	277 (197)
	Bluegill	70 (29)	82 (87)	96 (98)	112 (30)	124 (102)	126 (80)	141 (23)
Trout	Rock bass	75 (6)	90 (28)	103 (20)	128 (93)	147 (6)	157 (7)	185 (3)
	Perch	116 (158)	137 (87)	160 (29)	183 (24)	201 (5)	191 (4)	
	Common sucker	168 (2)	134 (20)	165 (12)	202 (25)	213 (15)	235 (43)	294 (32)
	Wall-eyed pike		189 (5)	266 (1)	227 (18)	310 (6)	308 (6)	338 (15)
Silver	Rock bass		89 (1)	102 (3)		132 (1)	160 (3)	157 (1)
	Perch	124 (463)	139 (102)	159 (63)	172 (4)			
	Common sucker	123 (2)	144 (3)	169 (9)	219 (1)	222 (5)	267 (7)	289 (26)

NEBISH LAKE

The collections from Nebish Lake contained significant numbers of only three species—rock bass (*Ambloplites rupestris*), yellow perch (*Perca flavescens*), and smallmouth black bass (*Micropterus dolomieu*)—in that order of abundance. A fourth

species, the largemouth black bass (*Aplites salmoides*) was represented by two individuals. These fish most probably had been introduced, since there is no evidence that Nebish Lake was supporting a population of largemouth black bass at the time the collections were made.

Tables 3, 4 and 5 contain data relative to the bathymetric distribution of the rock bass, yellow perch and smallmouth black bass in Nebish Lake in late summer. The dates of the collections were July 29 to August 6, 1931, and August 6 to 11, 1932. Sets were made at various localities in the lake (for map of Nebish Lake see Fig. 2). The fishing intensity (number of lifts) was distributed more irregularly among the different depths of water than would be desirable for a careful study of the vertical distribution of fish. However, the primary purpose of the fishing in Nebish Lake and the other lakes as well was the collection of specimens in quantity; consequently, the majority of the nets was set at depths at which experience had shown the best catches

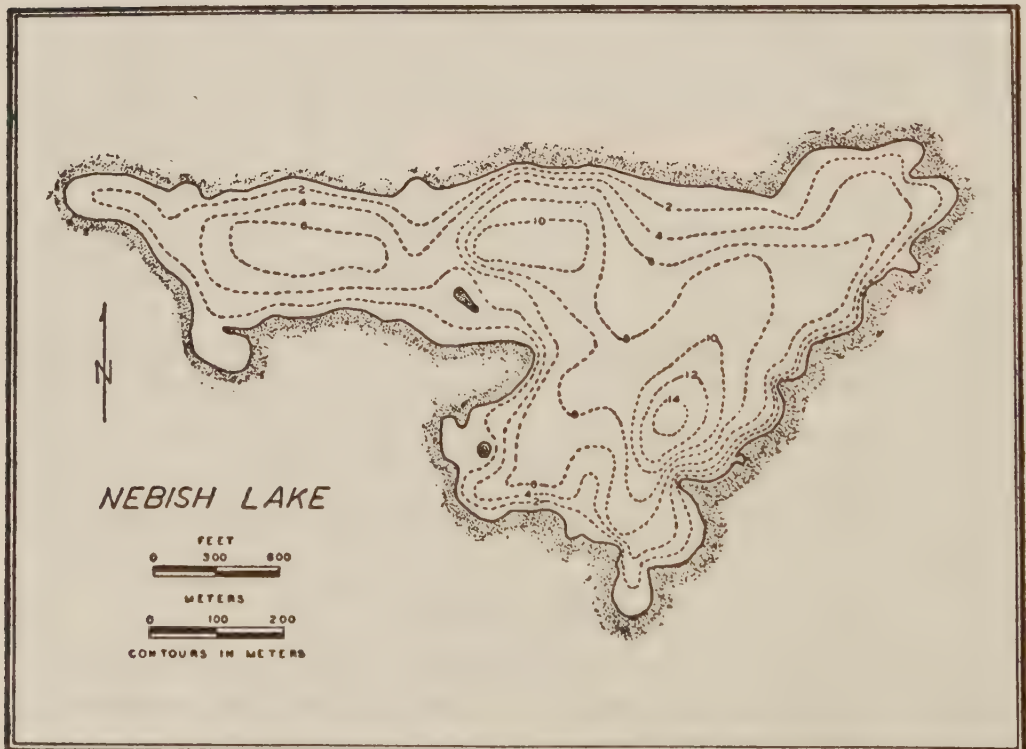


FIG. 2. Hydrographic map of Nebish Lake.

could be made. The combination of the data for 1931 and 1932 was made after an examination of the results for the two years separately failed to reveal significant differences.

The strata defined in Tables 3, 4 and 5 refer to the depths at which the nets were set on the bottom, not necessarily to the depths at which the fish were taken. Since the height of each net (distance between float-line and lead-line) was 6 feet as hung or approximately the depth of the strata of Tables 3, 4 and 5 (2 meters), a net set near the upper limit of an indicated stratum fished almost the entire stratum immediately above. On the other hand, the fishing of a net was confined to its own stratum only when it was set at the lower limit of that stratum. Consequently, nets set repeatedly and at random on the bottom within a 2-meter stratum actually fished on the average a water-stratum of nearly 4 meters. The average depth of the water-stratum fished corresponds approximately to the upper limit of the 2-meter stratum in which the nets were set. For example, the fishing of nets set in the stratum, 3.0 to 4.9 meters, extended through the stratum, 1.0 to 4.9 meters, and nets set at 5.0 to 6.9 meters fished the stratum, 3.0 to 6.9 meters. Because of the overlap in the depths fished by nets set in successive strata, the data of the type presented in Tables 3, 4 and 5 provide only an approximate measure of the bathymetric distribution of fish. It should be mentioned also that the depths employed in the analyses were the averages of the depths at the ends of the nets, (p. 150) and that different parts of the nets actually were set above and below the average depth. Errors from this source were reduced by the fact that nets were ordinarily set along rather than across the contours.

In order to avoid the too frequent use of such awkward expressions as "fish taken by nets set at 5.0 to 6.9 meters", the more simple term "fish taken at 5 meters" frequently will be employed. This latter phrase should be understood to refer to fish captured in a 4-meter stratum whose average depth was approximately 5 meters. In all tables of the type of Tables 3, 4 and 5 the upper limit of each stratum, which corresponds to the average depth at which the fish were captured by nets set in that particular stratum, has been printed in bold-face type. The average depth for the nets lifted from 11.0 meters and deeper is,

of course, indefinite. Nets fished in the stratum, less than 3.0 meters, took fish at an approximate average depth of 1.5 meters.

There is some evidence that in late July and early August large rock bass (Table 3) live in deeper water than do small ones. The best catches in all three of the smaller meshes ($1\frac{1}{4}$, $1\frac{1}{2}$, and $1\frac{3}{4}$ inches) were made at depths of 5 meters and less. The numbers of fish per lift were relatively low at 7 meters, and not one rock bass was taken in small-mesh nets at 9 meters or deeper. No lifts of the 2-inch mesh nets were made from the shallowest water and from 3.0 to 4.9 meters. The best catches (average of 6.4 fish per lift) were taken at 5 meters, but good lifts were made also at 7 meters (average of 4.5 fish). Nets of $2\frac{1}{4}$ -inch mesh took more fish at 9 meters than at shallower depths. Data are lacking for the $2\frac{1}{2}$ -inch mesh nets at 9 meters. The best lifts in this net were made at 5 meters, although good catches were taken also at lesser (3 meters) and greater (7 meters) depths. The catches of the 3-inch mesh net give the strongest support to the belief that the larger rock bass live in deeper water than do the smaller rock bass. The average catch at 7 meters (18.3 fish) was 3.2 times the average at 5 meters (5.7 fish), but was less than half the average at 9 meters (39.2

TABLE 3. *Average number of rock bass taken in Nebish Lake in nets set at different depths, 1931 and 1932 data combined. In parentheses, the number of lifts on which each average was based. Asterisks show strata at which the maximum average catches were taken.*

Depth in meters	Gill-net mesh (stretched measure)						
	$1\frac{1}{4}$ inches	$1\frac{1}{2}$ inches	$1\frac{3}{4}$ inches	2 inches	$2\frac{1}{4}$ inches	$2\frac{1}{2}$ inches	3 inches
<3.0	..	3.0	..	..	..	..	1.0
	..	(1)	..	..	..	..	(1)
3.0 to 4.9	2.0*	6.1	6.7*	..	1.0	8.5	..
	(2)	(7)	(3)	..	(1)	(2)	..
5.0 to 6.9	1.0	13.6*	5.1	6.4*	2.7	11.4*	5.7
	(5)	(8)	(7)	(8)	(9)	(9)	(7)
7.0 to 8.9	0.2	1.3	2.6	4.5	3.0	8.6	18.3
	(10)	(3)	(7)	(10)	(7)	(8)	(6)
9.0 to 10.9	0.0	..	0.0	0.5	3.7*	..	39.2*
	(1)	..	(2)	(2)	(3)	..	(4)
>10.9	0.0	0.0	..	..	..	0.0	0.0
	(1)	(1)	..	..	..	(1)	(1)

fish). No rock bass were taken from nets of any mesh size set at depths in excess of 10.9 meters.

Differences in the vertical distribution of perch according to size of fish, if present, were small (Table 4). The best catches of every mesh size were made at 3 or 5 meters. Nets of three of the four larger mesh sizes took their greatest catches at the lower of the above two depths, but the 3-meter depth was not represented in the lifts of the 2- and 3-inch mesh nets. Catches of the nets of all mesh sizes were reduced at 7 meters (no fish in the 3-inch mesh). Perch were very scarce or totally lacking in nets set at 9 meters, and none were caught in lifts from depths greater than 10.9 meters.

TABLE 4. Average number of yellow perch taken in Nebish Lake in nets set at different depths, 1931 and 1932 data combined. In parentheses, the number of lifts on which each average was based. Asterisks show strata at which the maximum average catches were taken.

Depth in meters	Gill-net mesh (stretched measure)						
	1¼ inches	1½ inches	1¾ inches	2 inches	2¼ inches	2½ inches	3 inches
<3.0		5.0 (1)					0.0 (1)
3.0 to 4.9	6.5* (2)	11.7* (7)	10.7* (3)		0.0 (1)	5.5* (2)	
5.0 to 6.9	4.0 (5)	9.2 (8)	7.7 (7)	3.6* (8)	1.2* (9)	1.1 (9)	0.3* (7)
7.0 to 8.9	2.8 (10)	2.7 (3)	6.7 (7)	3.1 (10)	0.7 (7)	0.4 (8)	0.0 (6)
9.0 to 10.9	0.0 (1)		0.5 (2)	0.0 (2)	0.3 (3)		0.2 (4)
>10.9	0.0 (1)	0.0 (1)				0.0 (1)	0.0 (1)

The results for the smallmouth black bass (Table 5) resemble those for the perch. All but one (2¼-inch mesh) of the different mesh sizes made their best catches in water shallower than 7 meters. The absence of smallmouth black bass in the deep-water lifts is in agreement with the observations for rock bass and perch.

The catch records of Tables 3, 4 and 5 indicate that to a large extent the rock bass, yellow perch and smallmouth black bass of

Nebish Lake were occupying a common habitat in late July and early August of 1931 and 1932. The only suggestion of segregation is found in the relatively deeper habitat of large rock bass.

TABLE 5. *Average number of smallmouth black bass aken in Nebish Lake in nets set at different depths, 1931 and 1932 data combined. In parentheses, the number of lifts on which each average was based. Asterisks show strata at which the maximum average catches were taken.*

Depth in meters	Gill-net mesh (stretched measure)						
	1¼ inches	1½ inches	1¾ inches	2 inches	2¼ inches	2½ inches	3 inches
<3.0		5.0* (1)					0.0 (1)
3.0 to 4.9	0.5 (2)	1.3 (7)	1.7* (3)		0.0 (1)	1.5* (2)	
5.0 to 6.9	2.4* (5)	0.5 (8)	0.6 (7)	1.2* (8)	0.9 (9)	1.1 (9)	0.9* (7)
7.0 to 8.9	0.2 (10)	0.0 (3)	1.1 (7)	0.8 (10)	1.0 (7)	0.1 (8)	0.5 (6)
9.0 to 10.9	0.0 (1)		0.0 (2)	0.5 (2)	2.0* (3)		0.0 (4)
>10.9	0.0 (1)	0.0 (1)				0.0 (1)	0.0 (1)

The complete absence of fish in the four lifts from depths of more than 10.9 meters suggests the presence of some barrier that prevented fish from penetrating the greater depths. A better idea of the probable location of the "barrier" may be had from a more exact knowledge of the depths from which the deep-water lifts were made. The 1¼- and 2½-inch mesh nets were lifted from a depth of 11 meters and, therefore, on the average, fished approximately the 9- to 11-meter stratum. The 1½-inch mesh net was lifted from a depth of 11.5 meters and fished the 9.5- to 11.5-meter stratum. The 3-inch mesh net, lifted from 12 meters of water, fished the 10- to 12-meter stratum. The logical location to assume for the hypothetical barrier would then appear to be at or slightly below 9 meters.

The factors that may be expected to exert the greatest influence on the vertical distribution of fish in inland lakes are the distribution of food organisms and the physical and chemical

TABLE 6. *Relationship between depth of water and temperature, hydrogen-ion concentration and the concentrations (milligrams per liter) of dissolved oxygen and free carbon dioxide in Nebish Lake on three dates in the summers of 1931 and 1932.*

Depth in meters	August 11, 1931				July 21, 1932				August 23, 1932			
	Temperature in °C.	O ₂	CO ₂	pH	Temperature in °C.	O ₂	CO ₂	pH	Temperature in °C.	O ₂	CO ₂	pH
0	22.3	7.7	0.7	7.5	19.5	8.2	1.5	6.6	22.1	8.2	1.6	6.8
2	21.8	..	..	..	..	..	..	..	..	..	..	..
3	21.0	..	..	..	19.5	7.9	1.5	6.6	22.0	8.3	1.6	6.8
5	20.8	8.1	0.7	7.5	19.4	8.2	1.5	6.6	21.3	8.0	1.6	6.6
6	20.6	..	..	..	19.3	..	..	..	..	7.9	1.6	6.7
7	20.3	8.1	1.0	7.5	15.0	8.4	2.0	6.5	20.8	7.8	2.1	6.4
8	13.7	7.6	1.2	7.3	13.0	7.4	4.5	6.2	17.7	3.3	10.6	6.2
9	13.2	..	..	..	11.2	5.7	6.5	6.2	13.5	1.0	13.6	6.1
10	12.5	0.7	10.2	6.7	10.2	3.1	8.5	6.1	12.2	0.65	15.1	6.0
11	11.2	..	..	..	9.6	2.6	9.0	6.1	11.0	0.55	15.6	6.1
12	10.4	0.2	13.5	6.7	9.0	1.45	10.0	6.1	10.1	0.4	16.6	6.1
13	..	..	..	..	..	0.4	11.0	6.1	9.6	0.4	20.6	6.1
14	..	0.2	16.0	6.7	8.8	0.9	11.0	6.0	..	0.2	21.6	6.1
15	9.9	..	16.0	6.7	..	..	..	..	..	..	..	..

¹ Temperature record for 15.5 meters.

conditions of the water. Although the food habits of the rock bass, perch and smallmouth black bass of Nebish Lake have been investigated (Couey, 1935), the lack of published data on the distribution of food organisms prevents an examination of the relationship between the bathymetric distributions of fish and their food. Neither is a vertical series of temperature readings and chemical determinations available for Nebish Lake during the periods in which the gill-net collections were taken (July 29-August 6, 1931, and August 6-11, 1932). However, the vertical series taken after the dates of the 1931 collections (on August 11) and both before and after the time of collection of the 1932 materials (July 21 and August 23) make possible a fairly satisfactory estimate of the conditions in Nebish Lake with respect to temperature, hydrogen-ion concentration and the concentrations of dissolved oxygen and free carbon dioxide at the time the gill-net samples were taken (Table 6).

The 9-meter contour which marks the approximate lowest depth to which fish penetrated in Nebish Lake in late July and early August, 1931 and 1932, fell in the thermocline on July 21 and August 23, 1932, and was below the thermocline on August 11, 1931. The thermal stratification of Nebish Lake on August 11 must be considered exceptional since a decline of 6.6° C. in temperature occurred between the depths of 7 and 8 meters whereas no other 1-meter stratum showed a decline of as much as 1° C. with the exception of the 10- to 11-meter stratum (decrease of 1.3° C.). It is not at all unlikely that a later disturbance of the water may have increased the thickness of the thermocline sufficiently to include the 9-meter contour.

The conditions in Nebish Lake at the time of the fishing operations were doubtless intermediate to those prevailing on July 21 and on the two August dates. It is likely therefore that near the end of July and in early August the depth of 9 meters lay near the lower limit of the region of abundant dissolved oxygen and near the upper limit of the region with high concentrations of free carbon dioxide. The changes in the hydrogen-ion concentration near the 9-meter depth were so small that they may be disregarded as a factor in the vertical distribution of fish in Nebish Lake. In fact, it appears that the variation in the hydrogen-ion concentration with depth of water is not suf-

ficiently great to affect significantly the bathymetric distribution of fish in any of the lakes considered in this study. Data on the hydrogen-ion concentration have been included chiefly to show the limited extent of the variations.

Low temperature of the water, a deficiency of oxygen or a high concentration of free carbon dioxide conceivably might limit the depth to which fish penetrate in Nebish Lake in mid-summer and late summer. More probably, a combination of some two or of all three factors played a deciding role. The "barrier" may have operated directly by calling forth an avoidance reaction on the part of the fish or indirectly through a control of the distribution of food organisms. The effectiveness of the barrier possibly may have been increased by the sharp gradients of temperature and/or of the concentrations of dissolved gases.

The observations of Pearse and Achtenberg (1920) have demonstrated that, for perch at least, a deficiency in oxygen does not constitute a barrier to movement into the deeper portions of a lake. On the basis of operations of experimental gill nets in Lake Mendota (Wisconsin) these authors reported that, "Though perch were usually most abundant immediately above the thermocline, large catches often occurred just below it, where there was no oxygen." The belief that perch could survive in oxygenless water over limited periods was substantiated by the experimental submersion (in cages) of a number of individuals in the region below the thermocline. Five of six specimens survived a period of 0.5 to 1.0 hour and two of six survived 2.0 to 2.5 hours, but none were alive after a 3-hour submersion. At the depth to which the cages were lowered, the oxygen content of the water was 0.05 cc. per liter (0.07 p. p. m.) and the concentration of free carbon dioxide was 5 cc. per liter (9.9 p. p. m.).

The observation of Pearse and Achtenberg that perch could not survive continued submersion in oxygen-deficient water was supported by the experiments of Smith (1924) who suspended fish in wire cages at various depths in Douglas Lake (Michigan). Smith employed a variety of species in his experiments, but perch were included in nearly all of the tests. Smallmouth black bass and rock bass were used only occasionally. Repeated tests indicated that the maximum depth at which fish can survive con-

tinued submersion is defined rather sharply; a distance of only 2½ feet may separate depths at which fish remain alive from depths at which conditions prove fatal. Smith stated that death occurred, "in water having decidedly less oxygen and less favorable acidity conditions, and these factors, rather than that of mere depth alone, determined the lowest limit at which fish could live." Although Smith made no definite statement as to the critical oxygen concentration, a careful examination of his data suggests that fish, particularly perch, were affected by oxygen concentrations of less than 3 or 4 p. p. m. The hydrogen-ion concentration in the shallowest water in which fish died did not fall below 7.1, and at no depth did the concentration fall below 6.8. Smith believed that the acidity conditions were not favorable at the depths at which fish died. It should be pointed out, however, that in Nebish Lake in 1932, perch, rock bass and smallmouth black bass were all abundant, indeed were compelled to live in waters that were more acid than those in which Smith held conditions to be unfavorable.

The experiments of Shelford and Allee (1913) on the reactions of fishes to gradients of dissolved atmospheric gases yielded direct evidence that fish do not exhibit a marked avoidance of water of low oxygen content, but that they do avoid high concentrations of free carbon dioxide. (Rock bass and smallmouth black bass were among the species with which the experiments were conducted.) From a long series of observations they concluded:

"It appears * * * that the importance of oxygen in determining the distribution of fish has been too much emphasized. * * * Fishes react to oxygen gradients, though usually indefinitely."

In the next paragraph they continued:

"On the other hand, the importance of carbon dioxide in fish distribution has been largely overlooked. It is significant that even in tap water, all the fish tried reacted very definitely to an amount of carbon dioxide that is scarcely greater than that often found in ponds. Increased carbon dioxide is usually accompanied in nature by low oxygen and it is to the combination of lack of oxygen * * * and increased carbon dioxide, that the fish react most definitely."

Wilding (1939) found the minimum amount of dissolved oxygen tolerated by perch to be 2.25 p. p. m. at temperatures of 20° to 26° C. He found, however, that "fish were capable of reducing the oxygen concentration to a lower level when the

temperature was reduced." The concentration of free carbon dioxide and the hydrogen-ion concentration were found to have no effect on the asphyxial oxygen concentration.

Powers (1938) pointed out that abnormally high concentrations of carbon dioxide may not be harmful to fish even at low concentrations of dissolved oxygen. He stated, "that the rock bass, *Ambloplites rupestris*, can absorb oxygen down to from about 0.40 to 0.30 milliliter per liter [0.57 to 0.42 p. p. m.] at pH 9.75 to 6.10 with the CO₂ tension from about 0.13 to about 21.00+ millimeters Hg [0.34 to 54.60+ p. p. m.]; the small-mouth bass, *Micropterus dolomieu*, down to about 0.40 to 0.30 milliliter per liter [0.57 to 0.42 p. p. m.] at pH 8.30 to 6.20± with the CO₂ tension from about 0.15 to 17.00+ millimeters Hg [0.40 to 44.21+ p. p. m.]; and the yellow perch, *Perca flavescens*, down to about 0.35± milliliters per liter [0.50± p. p. m.] at pH 8.60 to 6.50± with a CO₂ tension from about 0.15 to 14.00+ millimeters Hg [0.40 to 36.40+ p. p. m.]."³

In the same publication Powers emphasized the fact that, although fish can tolerate higher concentrations of free carbon dioxide than are ordinarily found in nature, they are nevertheless most sensitive to sudden changes in carbon dioxide tension. He considered the inability of fish to adjust themselves to alternating higher and lower carbon dioxide tensions an important source of sudden mortality in hatcheries and at times in natural waters.

It may be considered possible that the failure of fish to penetrate the deeper portions of Nebish Lake represents an avoidance reaction associated with the distress that accompanies the adjustment to a sharp change in carbon dioxide tension. On August 23, 1932, a marked upturn in the concentration of free carbon dioxide occurred at 8 meters and on August 11, 1931, an equally large upturn occurred between 8 and 10 meters. At the time of the collection of the samples, a similar gradient may have existed near the depth of 9 meters. Pearse and Achtenberg (1920) gave little information concerning the gradients of free carbon dioxide in the region of the thermocline and upper hypolimnion in Lake Mendota. However, their observations

³ The experiments upon which this statement was based are described in detail by Powers, Rostorfer, Shipe, and Rostorfer (1938).

that the concentrations of free carbon dioxide were 4.17 cc. per liter (8.2 p. p. m.) at 13.0 meters on August 10, 1916, and 5.0 cc. per liter (9.9 p. p. m.) at 13.5 meters from August 30 to September 4, 1916, indicate that the perch that entered the oxygen-deficient region below the thermocline were subjected to conditions that did not differ greatly from those in the upper part of the hypolimnion of Nebish Lake. Unquestionably different stocks of fish may react in a different manner to similar conditions; nevertheless the comparison of carbon dioxide concentrations in Nebish Lake and Lake Mendota throws doubt on the assumption that the relatively high concentration of free carbon dioxide constituted the barrier that prevented the movement of Nebish Lake fish into the deeper portions of the lake.

MUSKELLUNGE LAKE

The records of extensive fishing operations conducted with gill nets in Muskellunge Lake in 1931 and 1932 provide information on the distribution of fish in a larger lake and one with a greater variety of species than is found in Nebish Lake. Sets were made in four general localities in the lake (Fig. 3): (1) Crystal Bay; (2) Pearse Bay and the channel connecting it with the main body of the lake; (3) main body of the lake approximately off the northwest shore; and (4) extreme eastern portion of the main body of the lake. The species composition and the bathymetric distribution of fish in Pearse Bay and at the two stations in the lake proper agreed sufficiently well to warrant a combination of the data for the three localities. The data for the catches in Crystal Bay have been treated separately (p. 173). The dates of collection for the three stations that were combined were August 4 to 23, 1931, July 1 to July 16, 1932, and July 20 to August 5, 1932. Collections were taken in Crystal Bay, August 31 to September 4, 1931.

The significance of the arrangement of tabular material⁴ (Tables 8, 9 and 10) is the same as described previously for Nebish Lake (p. 152). Originally the catch records for stations

⁴It will be noticed in Tables 8, 9 and 10 that the total number of lifts of the 1¼-inch mesh net was considerably less than that of the nets of any other mesh size. Through a misunderstanding the 1¼-inch mesh net was, without our knowledge, omitted from the gangs during part of the 1932 season.

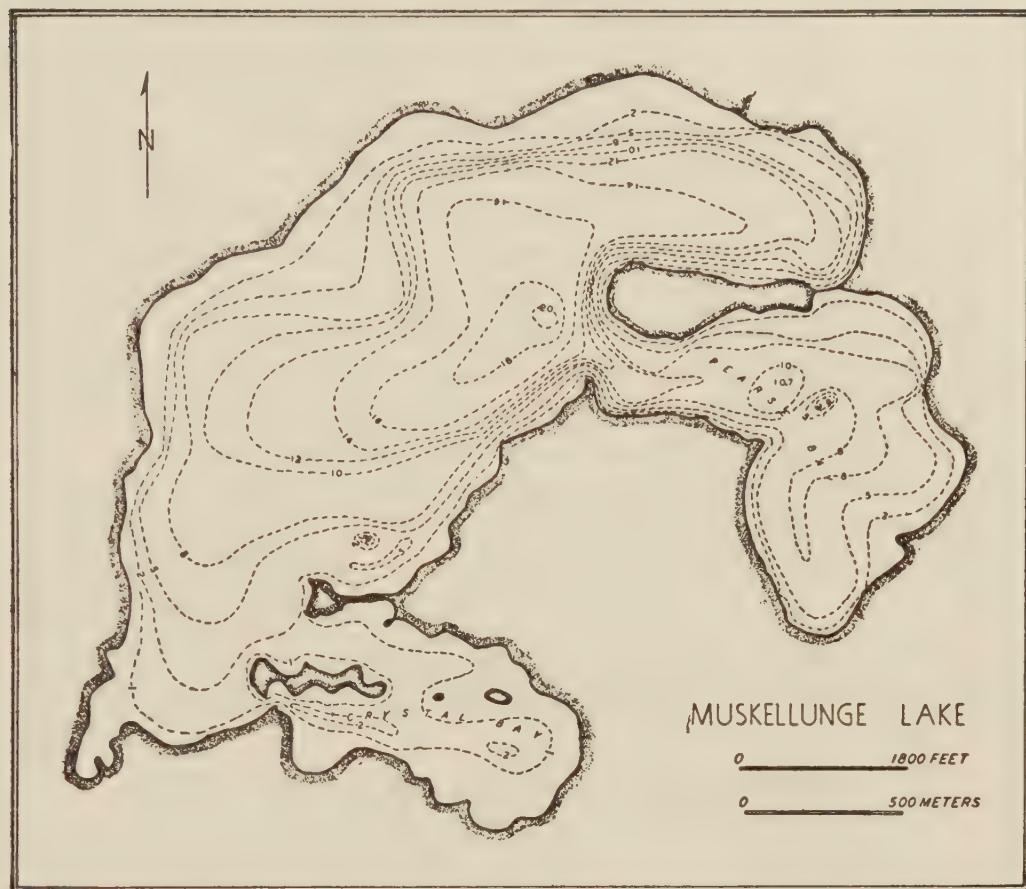


FIG. 3. Hydrographic map of Muskellunge Lake.

other than Crystal Bay were compiled separately for July and August. As no differences could be detected, the data for the two months have been combined.

Since the bathymetric distribution of fish in Muskellunge Lake will be discussed in relation to the physical and chemical conditions of the water, the presentation of distribution data for this lake will be preceded by the examination of vertical series of temperature readings and chemical determinations in July and August (Table 7). The thickness of the thermocline stratum was 3 or 4 meters on all four dates; however, the position of the thermocline was 2 meters deeper in late August than in early July. Dissolved oxygen was plentiful in the thermocline in July and was present in fair quantities in the upper 1 or 2 meters of the hypolimnion. Oxygen was relatively more abun-

TABLE 7. Relationship between depth of water and temperature, hydrogen-ion concentration and the concentrations (milligrams per liter) of dissolved oxygen and free carbon dioxide in Muskellunge Lake on four dates in 1931 and 1932

Depth in meters	July 10, 1931				August 26, 1931				July 5, 1932				August 25, 1932			
	Tempera- ture	O ₂	CO ₂	pH	Tempera- ture	O ₂	CO ₂	pH	Tempera- ture	O ₂	CO ₂	pH	Tempera- ture	O ₂	CO ₂	pH
0	21.2	8.6	1.0	7.1	20.2	8.6	0.2	7.5	18.6	8.3	1.2	7.4	21.3	8.0	1.0	7.5
3	...	8.5	...	...	...	8.5	0.2	7.5	...	8.7	1.2	7.4	...	...	1.0	8.0
5	21.0	8.6	1.0	7.1	...	8.8	...	...	18.6	8.1	1.2	7.4	21.3	8.7	1.0	7.6
6	21.0	8.6	1.0	7.1	20.2	8.5	0.3	7.5	18.5	8.7	1.2	7.4	...	...	1.0	...
7	19.6	8.6	1.0	...	20.0	8.5	0.5	7.4	16.6	8.4	1.7	7.3	...	...	1.2	...
8	16.5	8.6	1.2	7.1	19.7	6.7	0.5	7.3	13.5	9.4	2.2	7.2	...	8.2	2.0	7.4
9	14.0	5.7	...	...	17.8	7.6	3.0	6.8	12.6	8.8	2.7	7.2	20.7	...	4.5	...
10	12.9	5.6	6.5	6.3	14.8	1.6	7.5	6.8	11.8	6.6	4.5	6.9	17.8	5.3	8.0	7.1
11	11.8	5.4	6.7	...	13.0	1.1	10.0	...	11.3	...	...	...	14.5	2.7	12.5	6.7
12	11.2	3.6	8.6	6.3	12.0	0.2	11.5	6.7	10.9	0.7	11.5	6.7	13.8	0.4	16.5	6.5
13	10.9	...	...	...	11.2	...	...	...	...	...	...	...	10.5	0.6	16.5	6.4
15	10.2	...	...	6.3	10.2	0.0	13.5	6.7	...	0.6	11.5	6.5	...	...	20.0	6.4
17	10.0	0.3	11.0	6.3	...	...	...	6.7	10.2	0.2	12.0	6.5	...	0.6	...	...
18	...	...	...	...	...	0.0	14.0	6.7	...	...	...	...	...	...	...	...
19	...	...	...	...	...	...	...	...	...	0.2	...	6.5	...	...	21.5	6.4
20	...	...	...	...	...	0.0	15.5	6.7	9.5	...	13.0	...	...	0.2	21.5	6.4
20.5	...	...	...	...	9.8	...	...	...	...	...	...	...	10.1	...	...	...

dant at a greater depth on July 10, 1931, than on July 5, 1932. At 12 meters the concentration was 3.6 p. p. m. on the former date and only 0.7 on the latter. On August 26, 1931, a high concentration of dissolved oxygen was noted in only the upper meter of the thermocline. A day earlier in the next year, however, a pronounced deficiency was not found above the lowest meter of the thermocline. On all four dates the free carbon dioxide content of the water increased sharply in the thermocline; these increases were more rapid in August than in July. At almost all depths below 8 meters, for which the comparisons are available, the concentration of carbon dioxide was greater in August than in July and in 1932 than in the same month of 1931. The gradients of hydrogen-ion concentration in the thermocline were fairly sharp on all four dates. The total range of variation in hydrogen-ion concentration was much larger on August 25, 1932, than on the other dates.

The following general estimate of "average" conditions during the collecting season has been drawn from the data of Table 7:

- (1) The thermocline, which lay at approximately 7 to 11 meters, was characterized by a drop in temperature of about 8° C. (20° to 12°).

- (2) Dissolved oxygen was fairly plentiful at a depth as low as 10 meters (4 or 5 p. p. m.). A rapid decrease in oxygen content occurred below 10 meters, and the concentration was probably not in excess of 1 or 2 p. p. m. at 12 meters in 1931 and was below 1 p. p. m. in 1932. At lower depths oxygen was absent or in concentrations of less than 1 p. p. m. in both years.

- (3) The amount of free carbon dioxide increased rapidly in the thermocline and reached a concentration of 10 p. p. m. or more at 11 or 12 meters. Below the thermocline the increase in free carbon dioxide was continuous but more gradual.

- (4) There was a sharp gradient in the hydrogen-ion concentration in the thermocline. The total change in the thermocline nearly equalled the maximum difference between any two strata.

Tables 8, 9 and 10 contain the averages, according to mesh size and depth of water, of the numbers of individuals per lift for rock bass, perch and common suckers (*Catostomus commersonnii*), three of the four most abundant species in Muskellunge Lake. The data for the fourth species, the cisco (*Leucichthys artedi*),⁵ and for minor species are presented in Table 11 in terms of the total catch of a complete gang of seven nets (except in the shallowest and deepest strata where some mesh sizes were not represented).

The rock bass of Muskellunge Lake exhibits a distinct preference for a shallow-water habitat (Table 8). The best catches were made in less than 7 meters of water (the maximum of 5.0 fish per lift at 7 meters by the 1¾-inch mesh was matched by an equally large catch in 1.5 meters and good catches at 3 meters), and almost no rock bass were taken at 9 meters or deeper. If it is remembered that some of the nets lifted from the 7.0- to

TABLE 8. *Average number of rock bass taken in Muskellunge Lake in nets set at different depths, 1931 and 1932 data combined. In parentheses, the number of lifts on which each average was based. Asterisks show strata at which the maximum average catches were taken.*

Depth in meters	Gill-net mesh (stretched measure)							Total
	1¼ inches	1½ inches	1¾ inches	2 inches	2¼ inches	2½ inches	3 inches	
<3.0		2.0 (1)	5.0* (1)	0.0 (1)	2.0 (1)		3.0* (2)	12.0
3.0 to 4.9	1.8 (4)	8.1* (12)	4.3 (11)	1.8 (13)	2.3* (12)	5.3* (11)	2.3* (9)	25.9*
5.0 to 6.9	2.5* (11)	5.2 (20)	3.3 (21)	2.5* (21)	2.2 (21)	2.1 (20)	1.5 (19)	19.3
7.0 to 8.9	0.8 (6)	0.8 (5)	5.0* (3)	0.5 (4)	0.8 (4)	1.4 (10)	1.7 (9)	11.0
9.0 to 10.9	0.0 (8)	0.0 (6)	0.4 (11)	0.0 (8)	0.2 (6)	0.0 (6)	0.0 (5)	0.6
11.0 to 12.9	0.0 (1)	0.0 (5)	0.0 (2)	2.0 (1)	0.0 (1)	0.0 (1)	0.0 (1)	2.0
13.0 to 14.9	0.0 (2)	0.0 (1)		0.0 (2)				0.0

⁵ The data on the bathymetric distribution of the cisco have been summarized from detailed information presented in an earlier paper (Hile, 1936). Only three sizes of gill-net mesh (1¼, 1½ and 1¾ inches) took ciscoes in Muskellunge Lake. The majority was captured by the 1½-inch mesh net.

8.9-meter stratum may have fished almost up to the 5-meter depth, it appears likely that the upper limit of the thermocline marks the approximate lower limit of the habitat occupied by the mass of the rock bass population.

The failure of any important portion of the rock bass stock to enter the region of the thermocline is in disagreement with the situation in Nebish Lake where large numbers of fish were captured near 9 meters, well into the thermocline. A second difference between the two lakes is to be found in the relationship of size of fish to the depth of water inhabited. There is little or no indication that size has any bearing on the depth of water in which Muskellunge Lake rock bass live. In Nebish Lake, on the contrary, there was a definite tendency for the larger rock bass to live at a greater depth than the small ones. This difference in the distribution of rock bass in the two lakes possibly may depend on differences in the distribution of the food organisms taken by rock bass of various sizes.

The outstanding feature in the bathymetric distribution of perch in Muskellunge Lake (Table 9) is the clear-cut relationship between the size of fish and the depth of water inhabited. The smallest perch caught, that is, those captured in the 1¼-inch mesh, were most abundant at about 11 meters. Each increase in mesh size from the 1¼-inch to the 2-inch mesh was accompanied by a 2-meter decrease in the depth at which the largest catches of perch were taken. There was no consistent relationship between size of mesh and depth of maximum catch in the four larger mesh sizes. However, three of the four larger mesh sizes took their best catches at 5 meters or shallower. The great difference between the distributions of large and small perch is brought out by the comparison of the total catch at different depths of the nets with the two smaller and the five larger mesh sizes. A difference of 6 meters separates the depths at which the two groups of nets made their maximum catches.

The pronounced tendency for the smaller perch to inhabit the deeper water of Muskellunge Lake stands in marked contrast to the distribution of perch in Nebish Lake. With the exception of a possible tendency for the smaller perch to inhabit slightly shallower water than the larger ones, there was no apparent correlation between the size of Nebish Lake perch and

TABLE 9. Average number of yellow perch taken in Muskegon Lake in nets set at different depths, 1931 and 1932 data combined. In parentheses, the number of lifts on which each average was based. Asterisks show strata at which the maximum average catches were taken.

Depth in meters	Gill-net mesh (stretched measure)								Total for meshes		
	1 1/4 inches	1 1/2 inches	1 3/4 inches	2 inches	2 1/4 inches	2 1/2 inches	3	1 1/4 and 1 1/2 inches	Above 1 1/2 inches	All	
<3.0	..	7.0 (1)	1.0 (1)	0.0 (1)	0.0 (1)	..	0.0 (2)	7.0	1.0	8.0	
3.0 to 4.9	6.3 (3)	3.8 (12)	0.9 (11)	0.3 (13)	0.3 (12)	0.1 (11)	0.8* (9)	10.1	2.4	12.5	
5.0 to 6.9	19.7 (11)	3.9 (20)	1.6 (21)	1.3* (21)	1.4* (21)	0.4 (20)	0.1 (19)	23.6	4.8*	28.4	
7.0 to 8.9	51.2 (5)	9.4 (5)	2.0* (3)	0.8 (4)	1.0 (4)	0.8* (10)	0.1 (9)	60.6	4.7	65.3	
9.0 to 10.9	159.9 (8)	17.0* (6)	0.7 (11)	0.4 (8)	0.2 (6)	0.3 (6)	0.4 (5)	176.9	2.0	178.9	
11.0 to 12.9	181.0* (1)	15.8 (5)	0.0 (2)	1.0 (1)	0.0 (1)	0.0 (1)	0.0 (1)	196.8*	1.0	197.8*	
13.0 to 14.9	43.0 (2)	0.0 (1)	..	0.5 (2)	..	..	..	43.0	0.5	43.5	

the depth at which they occurred (p. 155). With the perch as with the rock bass, differences in the distribution of food taken by individuals of various sizes appear to offer the most logical explanation of the differences in the distribution of fish in the two lakes.

It is not known whether perch penetrate to greater depths than those fished by nets set at 13.0 to 14.9 meters. The only direct evidence on this question is contained in the records for a string of nets (including the mesh sizes, $1\frac{1}{2}$ and 2 inches) lifted from 17.5 meters on August 27, 1930. The total catch was a single sucker, which was dead at the time the nets were lifted. The limnological data of Table 7 throw doubt on the ability of perch to maintain themselves continuously at depths in excess of, at most, 12 meters. The detailed records for the two lifts of $1\frac{1}{4}$ -inch mesh nets from the 13.0- to 14.9-meter stratum offer evidence that some of the perch taken in these nets may have been captured during a temporary excursion into an oxygen-deficient region. The shallower of the two lifts, which contained 56 perch, was made off the north shore on August 4, 1932, from a depth of 13.2 meters. Since the net was 6 feet or nearly 2 meters deep it fished water as shallow as 11 meters. The deeper lift (containing 30 perch) was made on July 29, 1932, near the eastern end of the lake from a depth of 14.5 meters. Fish taken in this net were therefore captured at average depths in excess of 12.5 meters. If it is assumed that all perch were captured near the top of the net (no records were kept of the position of fish in the nets) it may be considered possible that the perch of the August 4 collection were captured in water with a sufficient supply of dissolved oxygen to maintain life. The perch from the deeper lift of July 29 were very probably taken in water that was deficient in oxygen (less than 1 p. p. m.). It is possible therefore that in Muskellunge Lake as in Lake Mendota (Pearse and Achtenberg, 1920) perch may spend short periods of time in oxygen-deficient regions.

Suckers were taken in greatest abundance at 7 and 9 meters, except in the $1\frac{1}{4}$ -inch mesh nets whose catches were negligible (Table 10). There is indication that the larger suckers lived in the deeper water. Nets of the mesh sizes, $1\frac{1}{2}$, $1\frac{3}{4}$ and 2 inches, took their largest catches at 7 meters. In the nets with

the three larger meshes, however, the averages at 9 meters were from two to four times as large as those for the nets with the same sizes of mesh at 7 meters. Very few suckers were taken at 11 meters or deeper.

TABLE 10. *Average number of common suckers taken in Muskellunge Lake in nets set at different depths, 1931 and 1932 data combined. In parentheses, the number of lifts on which each average was based. Asterisks show strata at which the maximum average catches were taken.*

Depth in meters	Gill-net mesh (stretched measure)							Total
	1¼ inches	1½ inches	1¾ inches	2 inches	2¼ inches	2½ inches	3 inches	
<3.0		0.0 (1)	2.0 (1)	2.0 (1)	2.0 (1)		2.0 (2)	8.0
3.0 to 4.9	0.0 (4)	2.3 (12)	1.6 (11)	2.0 (13)	2.5 (12)	3.4 (11)	3.1 (9)	14.9
5.0 to 6.9	0.3* (11)	2.0 (20)	2.0 (21)	2.2 (21)	3.7 (21)	4.7 (20)	2.2 (19)	17.1
7.0 to 8.9	0.0 (6)	6.8* (5)	5.0* (3)	4.7* (4)	7.2 (4)	7.4 (10)	1.8 (9)	32.9
9.0 to 10.9	0.1 (8)	0.0 (6)	2.6 (11)	4.4 (8)	14.4* (6)	14.7* (6)	7.2* (5)	43.4*
11.0 to 12.9	0.0 (1)	0.0 (5)	0.0 (2)	4.0 (1)	0.0 (1)	0.0 (1)	4.0 (1)	8.0
13.0 to 14.9	0.0 (2)	0.0 (1)		0.0 (2)				0.0

Diurnal inshore and offshore movements may have affected the data on the bathymetric distribution of suckers in Muskellunge Lake. Evidence for a daily migration of suckers in this lake was obtained by Spoor and Schloemer (1939) from a series of 10 sets of gill nets⁶ (usually along the 6-meter contour) in the summers of 1933 to 1937. Examinations at 2- to 4-hour intervals revealed that from midnight to noon the majority of suckers had entered the nets from the shore side (that is, were moving toward deeper water), whereas from noon to midnight the majority had entered the nets from the lake side (were moving inshore). However, the clear-cut relationship between the depth of water and the number of suckers taken in 24-hour

⁶ Except for the omission of the 1¼-inch mesh net the gear employed by Spoor and Schloemer included the same mesh sizes as those fished in 1931 and 1932.

sets (Table 10) indicates that the diurnal movements described by Spoor and Schloemer were either limited in their vertical extent or were undertaken by only part of the individuals in the population.

Spoor and Schloemer were unable to detect diurnal inshore and offshore movements in the Muskellunge Lake rock bass. They concluded that the movements of rock bass near the 6-meter contour were purely random.

Table 11 provides a composite picture of the bathymetric distribution of seven species of fish in Muskellunge Lake, exclusive of Crystal Bay. The values in the table represent the total catch of a complete gang of seven nets (except for the perch which were divided into groups of "small" and "large" fish—see Table 9) for all strata from 3 to 11 meters. Two mesh sizes are not represented in the lifts from less than 3 meters and four in the lifts from 13.0 to 14.9 meters.

Four species—rock bass, smallmouth black bass, bluegills (*Lepomis macrochirus*), and largemouth black bass—were most abundant at approximately 3 meters. All of these species may be said to inhabit the warm water of the epilimnion. The larger perch live in slightly deeper water than the four shallow-water species. The greatest numbers were captured at 5 meters but almost equally large catches were taken at 7 meters. Small perch, however, were most plentiful in deep water at 9 and 11 meters. It is of interest that the best catches of both perch and ciscoes were obtained at 11 meters. This situation emphasizes the apparent preference of small perch for deep, cold water. The presence of ciscoes at 13 meters indicates that this species as well as the perch may penetrate waters that are deficient in oxygen. Suckers were most abundant between the regions inhabited by the shallow-water species and by the small perch and ciscoes. The depths of greatest abundance of suckers (7 and 9 meters) correspond roughly to the upper portion of the thermocline.

The relationships indicated by the data of Table 11 apply, of course, to the summer only. At other seasons—in winter and at the periods of turnover—the distribution of the various species is probably much different.

TABLE 11. Number of individuals of seven species taken in gill nets set at different depth in Muskellunge Lake in July and August, 1931 and 1932. The numbers represent the average catch of a complete gang of seven different mesh sizes in all strata except "less than 3.0" and "13.0 to 14.9 meters." The asterisks indicate the strata of maximum abundance.

Depth in meters	Species ¹							
	Rock bass	Smallmouth black bass	Perch		Bluegills	Largemouth black bass	Suckers	Ciscoes
			Small	Large				
<3.0	12.0	3.0	7.0	1.0	0.0	0.0	8.0	0.0
3.0 to 4.9	25.9*	4.1*	10.1	2.4	3.2*	0.6*	14.9	0.2
5.0 to 6.9	19.3	3.7	23.6	4.8*	1.8	0.3	17.1	0.1
7.0 to 8.9	11.0	3.2	60.6	4.7	0.4	0.0	32.9	12.5
9.0 to 10.9	0.6	0.4	176.9	2.0	0.0	0.0	43.4*	40.8
11.0 to 12.9	2.0	0.0	196.8*	1.0	0.0	0.0	8.0	135.9*
13.0 to 14.9	0.0	0.0	43.0	0.5	0.0	0.0	0.0	18.5
								31.0
								61.4
								70.7
								125.3
								264.1
								343.7*
								62.0

¹ In addition to the catches listed in the table there were taken: four wall-eyed pike (*Stizostedion vitreum*) at depths less than 7 meters; one muskellunge (*Esox masquinongy*) at 6 meters; and one miller's thumb (Cottidae) at 3 meters.

The results of five lifts of complete gangs of gill nets⁷ in Crystal Bay are summarized in Table 12. No separations of the catches as to depth were made since practically all of the Bay is less than 2 meters deep. Ecologically Crystal Bay is distinctly different from the remainder of Muskellunge Lake. The shallower water of most of the lake is characterized by a sand and gravel bottom, with a limited amount of submerged vegetation offshore. In Crystal Bay, on the contrary, the mucky bottom is covered with a dense growth of vegetation.

TABLE 12. Average number of individuals of four species taken per day in different sizes of mesh of gill nets set in Crystal Bay, Muskellunge Lake, over the 5-day period, August 31 to September 4, 1931.

Species ¹	Gill-net mesh (stretched measure)							Total
	1¼ inches	1½ inches	1¾ inches	2 inches	2¼ inches	2½ inches	3 inches	
Rock bass	8.4	7.0	2.2	5.8	7.0	5.0	1.6	37.0
Perch	12.0	2.0	1.2	0.2	0.8	0.4	0.0	16.6
Sucker	5.6	2.2	1.4	1.8	5.0	6.6	7.0	29.6
Bluegill	1.6	2.4	11.2	3.0	11.4	5.6	2.2	37.4

¹ The total catches per gang per day of species other than those listed in the table were: golden shiner (*Notemigonus crysoleucas*)—2.8; mud minnow (*Umbriidae*)—0.4; largemouth black bass—0.4; muskellunge—0.2.

The ecological nature of the Crystal Bay habitat is reflected in the generally greater abundance of fish and particularly in the presence of large numbers of bluegills. The total numbers of fish in Tables 11 and 12 for a gang of nets in shallow water are not comparable since two mesh sizes were lacking in the data for the lake proper. A more reliable comparison may be had from the following tabulation in which the catches of the 1¼-inch and 2½-inch mesh nets have been omitted from the totals for Crystal Bay:

Average Total Catch of Nets of Five Mesh Sizes

Species	Crystal Bay	Lake proper
Rock bass	23.6	12.0
Perch	4.2	8.0
Sucker	17.4	8.0
Bluegill	30.2	0.0

⁷ The five lifts do not represent the total fishing effort in Crystal Bay in 1931 and 1932 but include merely the 24-hour sets. At the time of the earlier 1931 operations and in 1932 the number of persons in the State tourist camp, which is located on the Bay, made it inadvisable to leave gill nets unguarded in such shallow water. Consequently the nets were set for only short periods and on some occasions the fish were driven into them by beating the surface of the water with poles and by the noise of an outboard motor.

It is believed that the above data on the catches of fish in Crystal Bay and in the shallow water of the open lake (including Pearse Bay) are comparable in spite of the fact that the fishing operations in Crystal Bay were carried out somewhat later in the season than were those in the lake proper (August 31 to September 4, 1931, in the Bay as compared to August 4 to August 23, 1931, and July 1 to July 16, 1932, and July 29 to August 5, 1932). Operations with gill nets set for short periods on August 17 and 28, 1931, and August 26 to 31, 1932, gave no indication that either the species composition or the abundance of fish in Crystal Bay was undergoing a change in late August. Rock bass and suckers were approximately twice as abundant in Crystal Bay as in the shallow water of the open lake but only half as many perch were taken in the Bay. Bluegills, which were absent in shallow water in the open lake and were scarce at greater depths (Table 11), were the dominant species in the Crystal Bay catches. The Crystal Bay catches were featured also by the total absence of smallmouth black bass and the presence of a number of golden shiners (total of 14 in all nets for the 5-day period).

OTHER LAKES

Records of fishing operations in 1930, 1931 and 1932 have made available a small amount of information on the bathymetric distribution of fish in three additional lakes (Trout, Silver and Clear) in the northeastern highland region. Although the data are extremely scanty, they do provide some instructive comparisons with the more detailed data from Nebish Lake and Muskellunge Lake.

Trout Lake. The average lifts of four species of fish—rock bass, perch, suckers and wall-eyed pike—in the shallower water of Trout Lake are listed in Table 13. The nets on whose catches the table was based were set in both basins a short distance from the channel connecting the two. The dates of collection were July 23 and 24, 1931, and August 10 to 13, 1932. In spite of the low fishing intensity the rock bass may be said to occur in greatest abundance in relatively shallow water at approximately 3 meters. (The only net set in still shallower water took no rock bass.) The single individual that was taken in a net lifted

from 10.0 meters may be considered a straggler. Perch were taken in greater numbers at 3 than at 5 meters. The nets set in deeper water had too large meshes to sample the perch stock satisfactorily. Suckers exhibited differences in distribution correlated with the size of the fish. Nets with the four smaller meshes made their best catches at 3 meters but those with the larger meshes were most successful in water 2 to 4 meters deeper (*cf.* Muskellunge Lake, p. 170). The smaller mesh nets, in gen-

TABLE 13. *Average number of each of four species of fish taken in Trout Lake in nets set at different depths, 1931 and 1932 data combined. In parentheses, the number of lifts on which each average was based. Asterisks show strata at which the maximum average catches were taken.*

Depth in meters ¹	Rock bass in gill-net mesh (stretched measure)						
	1¼ inches	1½ inches	1¾ inches	2 inches	2¼ inches	2½ inches	3 inches
<3.0				0.0 (1)			
3.0 to 4.9	6.0* (1)	1.5* (4)	14.0* (1)	14.5* (2)	4.0* (1)	0.0 (1)	0.0 (1)
5.0 to 6.9	0.2 (4)	0.0 (2)	0.8 (5)	0.3 (3)	0.3 (3)	0.0 (3)	0.3 (3)
7.0 to 8.9					0.0 (1)	0.0 (1)	0.0 (1)
9.0 to 11.9						0.0 (1)	1.0* (1)
Depth in meters	Perch in gill-net mesh (stretched measure)						
	1¼ inches	1½ inches	1¾ inches	2 inches	2¼ inches	2½ inches	3 inches
<3.0				2.0 (1)			
3.0 to 4.9	32.0* (1)	17.5* (4)	17.0* (1)	6.0* (2)	3.0* (1)	1.0* (1)	0.0 (1)
5.0 to 6.9	16.8 (4)	6.5 (2)	2.2 (5)	2.3 (3)	0.3 (3)	0.3 (3)	0.0 (3)
7.0 to 8.9					0.0 (1)	0.0 (1)	0.0 (1)
9.0 to 11.9							0.0 (1)

¹ The sets at 9.0 to 11.9 were: 2½-inch mesh net at 11.8 meters; 3-inch mesh net at 10.0 meters. The 2½-inch mesh net took nine whitefish. Other fish not listed in the table were one largemouth black bass at 3 meters and one redhorse sucker (*Moxostoma*) at 4 meters.

Depth in meters	Suckers in gill-net mesh (stretched measure)						
	1¼ inches	1½ inches	1¾ inches	2 inches	2¼ inches	2½ inches	3 inches
<3.0				0.0 (1)			
3.0 to 4.9	1.0* (1)	0.8* (4)	4.0* (1)	4.5* (2)	3.0 (1)	2.0 (1)	5.0 (1)
5.0 to 6.9	0.0 (4)	0.0 (2)	1.6 (5)	1.0 (3)	1.0 (3)	5.7* (3)	6.0* (3)
7.0 to 8.9					6.0* (1)	1.0 (1)	2.0 (1)
9.0 to 11.9						0.0 (1)	0.0 (1)
Depth in meters	Wall-eyed pike in gill-net mesh (stretched measure)						
	1¼ inches	1½ inches	1¾ inches	2 inches	2¼ inches	2½ inches	3 inches
<3.0				0.0 (1)			
3.0 to 4.9	0.0 (1)	0.0 (4)	0.0 (1)	1.0* (2)	0.0 (1)	0.0 (1)	3.0 (1)
5.0 to 6.9	0.0 (4)	0.0 (2)	0.2* (5)	0.0 (3)	1.0 (3)	0.3 (3)	0.7 (3)
7.0 to 8.9					3.0* (1)	2.0* (1)	4.0* (1)
9.0 to 11.9						0.0 (1)	1.0 (1)

eral, failed to take wall-eyed pike. Nets with the three larger mesh sizes were most successful at 7 meters (only one lift of each mesh size).

The rock bass of Trout Lake inhabits approximately the same depth of water as in Muskellunge Lake (greatest abundance at about 3 meters), but lives in shallower water than do the larger rock bass of Nebish Lake. On the other hand, perch were most plentiful in lifts from approximately 3 meters in both Trout Lake and Nebish Lake but were most abundant at greater depths in Muskellunge Lake. The smaller Muskellunge Lake perch in particular appeared to prefer deep water (9 to 11 meters). Suckers live in shallower water in Trout Lake (about 3 to 5 meters) than in Muskellunge Lake (7 to 9 meters). The

two lakes show a similar correlation between the size of suckers and the depth at which they live (with the larger fish in the deeper water).

Fishing operations were carried on in 1930 with the "old" nets (see p. 150) in Blaisdell's Bay at the extreme southeast corner of Trout Lake at depths of about 5 meters and shallower. Records of depth were not obtained for the individual nets, but the catch indicates a species composition in the shallow water similar to that in the neighborhood of the channel connecting the two basins of the lake. The total 1930 catch in Blaisdell's Bay consisted of 93 perch, 27 common suckers, 20 rock bass, 12 wall-eyed pike and 1 smallmouth black bass.

Fishing operations were carried on in the hypolimnion of the south basin of Trout Lake in July, 1930 and 1931, at depths of from 15 to 33.5 meters. Only typically deep-water forms—ciscoes, whitefish (*Coregonus clupeaformis*), lake trout (*Cristivomer n. namaycush*) and burbot (*Lota maculosa*)—were taken.⁸ Since the conditions with respect to the dissolved gases,

TABLE 14. Relationship between depth of water and temperature, hydrogen-ion concentration and the concentrations (milligrams per liter) of dissolved oxygen and free carbon dioxide in Trout Lake, August 10, 1931.

Depth in meters	Temperature in °C.	O ₂	CO ₂	pH
0	20.6	8.3	1.0	7.7
5	..	8.5	1.0	7.7
8	20.6	8.4	1.0	7.7
9	20.2	8.5	1.0	7.7
10	16.2	8.4	1.5	7.5
11	13.4	..	..	..
12	11.7	..	..	..
14	10.3	..	..	..
15	9.8	8.5	3.7	7.4
18	8.6	..	..	..
20	8.3	6.2	5.5	7.1
25	7.7	5.0	7.5	7.0
28	..	3.6	8.5	7.0
30	..	3.4	9.7	..
31	..	3.0	9.7	6.9
32	..	2.1	11.0	6.9
32.5	7.2	..	11.0	6.9

⁸ The actual numbers were: ciscoes—1,197; whitefish—32; lake trout—32; burbot—1 (Hile 1936).

oxygen and carbon dioxide, are satisfactory in most of the hypolimnion in the summer (Table 14), the absence of shallow-water fish was probably due to the low water temperatures, or the scarcity or absence of their favorite food organisms.

Silver Lake. The scarcity of rock bass and suckers in Silver Lake together with the small number of gill nets lifted renders the formation of conclusions as to the bathymetric distribution of these species⁹ inadvisable. The data of Table 15 serve chiefly to show the presence of a dense concentration of perch at 5 and 7 meters under late-summer conditions. (The dates of collection were August 20 to 24, 1931, and August 16, 1932.) Further information on the distribution of fish in Silver Lake was obtained from the catches of gill nets that were set in deeper water for the capture of ciscoes. (The dates of these deep-water lifts were August 9, 10 and 15, 1930, and July 17 and August 22, 1931.) These nets took 524 ciscoes—all from nets that were lifted from depths between 10.5 and 15.5 meters. The only fish taken along with the ciscoes was a perch captured at 14.5 meters.

The Silver Lake cisco was most abundant at approximately the same depth of water in summer as the Muskellunge Lake cisco. However, the Muskellunge Lake cisco is forced to share its summer habitat with other forms, particularly small perch, whereas in Silver Lake the cisco lives practically in isolation. This difference in the distribution of fish in the two lakes appears difficult to explain on the basis of temperatures and the concentrations of dissolved gases (Tables 7 and 16). The conditions with respect to the dissolved gases in the lower thermocline and upper hypolimnion of Silver Lake in late August were distinctly superior to those in Muskellunge Lake.¹⁰ It is true that the temperatures in Silver Lake were somewhat lower than at corresponding depths in Muskellunge Lake. However, this temperature difference appears less important when it is remembered that in Muskellunge Lake the small perch were taken in the coldest water that contained sufficient oxygen to support

⁹ In addition to the fish listed in Table 15, there were taken 10 small-mouth black bass at depths of 3 to 7 meters and one cisco (in 1932) at 6 meters.

¹⁰ The most reliable comparison with the Silver Lake data of August 28, 1931, is to be had from the two Muskellunge Lake series taken in August (Table 7).

TABLE 15. Average number of each of three species of fish taken in Silver Lake in nets set at different depths, 1931 and 1932 data combined. In parentheses, the number of lifts on which each average was based.

Depth in meters	Rock bass in gill-net mesh (stretched measure)						
	1¼ inches	1½ inches	1¾ inches	2 inches	2¼ inches	2½ inches	3 inches
3.0 to 4.9				0.0 (1)	0.3 (3)	0.0 (3)	0.2 (4)
5.0 to 6.9	0.0 (2)	0.0 (2)	0.0 (1)	0.0 (2)	0.3 (3)	0.0 (1)	
7.0 to 8.9		1.0 (1)	1.5 (2)			1.5 (2)	0.0 (2)
Depth in meters	Perch in gill-net mesh (stretched measure)						
	1¼ inches	1½ inches	1¾ inches	2 inches	2¼ inches	2½ inches	3 inches
3.0 to 4.9				1.0 (1)	0.3 (3)	0.0 (3)	0.0 (4)
5.0 to 6.9	128.5 (2)	64.0 (2)	5.0 (1)	3.5 (2)	0.0 (3)	2.0 (1)	
7.0 to 8.9		77.0 (1)	38.0 (2)			0.0 (2)	0.0 (2)
Depth in meters	Suckers in gill-net mesh (stretched measure)						
	1¼ inches	1½ inches	1¾ inches	2 inches	2¼ inches	2½ inches	3 inches
3.0 to 4.9				0.0 (1)	1.0 (3)	1.0 (3)	3.0 (4)
5.0 to 6.9	0.5 (2)	0.0 (2)	4.0 (1)	0.0 (2)	0.7 (3)	2.0 (1)	
7.0 to 8.9		3.0 (1)	2.5 (2)			1.5 (2)	7.5 (2)

life and may even have spent short periods of time at levels deficient in oxygen. In Silver Lake, again, the lack of data prevents an examination of the possible effects of the distribution of food organisms on the distribution of fish.

Clear Lake. Almost all of the fishing operations in Clear Lake were conducted in the deep water in July, August and early September, 1931 and 1932, for the capture of ciscoes. Individuals of this species were taken in Clear Lake in nets set as shallow as 8 meters, but most of them were captured in the

hypolimnion between the depths of 15 and 25 meters. The outstanding feature of the Clear Lake catches was the presence of wall-eyed pike at all depths at which the cisco occurred. Thirty-seven wall-eyed pike were taken in the same nets that captured 465 ciscoes. Although the summer conditions in deep water are generally similar in Clear Lake (Table 17) and Trout Lake (Table 14), wall-eyed pike were not taken in the hypolimnion of the latter lake. Other fish taken in the hypolimnion of Clear Lake were one rock bass (at 15.5 meters) and five perch (19.5 to 24.5 meters). These two species also were absent from the hypolimnion of Trout Lake. A short gang of "old" nets of mesh sizes $1\frac{1}{2}$ and 2 inches set in shallow water on September 5, 1931, took 12 perch, 1 rock bass, 2 wall-eyed pike and 2 smallmouth black bass.

TABLE 16. *Relationship between depth of water and temperature, hydrogen-ion concentration and the concentrations (milligrams per liter) of dissolved oxygen and free carbon dioxide in Silver Lake, August 28, 1931.*

Depth in meters	Temperature in °C.	O ₂	CO ₂	pH
0	20.2	8.7	0.7	7.7
5	20.2	8.9	0.7	7.7
6	..	8.8	0.7	..
7	20.2	9.2	0.5	7.7
8	18.8	9.9	0.5	7.7
9	14.7	13.2	0.2	7.8
10	11.4	11.7	1.5	7.5
11	9.4	9.8	3.0	7.4
12	8.6	7.5	6.0	7.3
13	..	4.4	9.5	7.1
14	7.7	1.6	12.0	6.9
15	7.2	0.6	13.0	6.9
17	..	0.0	23.5	6.9
18	..	0.0	31.0	6.9
19	6.8	..	..	..

TABLE 17. *Relationship between depth of water and temperature, hydrogen-ion concentration, and the concentrations (milligrams per liter) of dissolved oxygen and free carbon dioxide in Clear Lake, August 19, 1932.*

Depth in meters	Temperature in °C.	O ₂	CO ₂	pH
0	20.9	8.1	2.0	6.5
5	20.9	7.9	2.0	6.5
10	18.5	8.1	2.0	6.5
12	12.4	9.5	3.0	6.4
15	9.9	7.9	5.5	6.2
20	8.6	6.0	7.5	6.1
23	8.4	4.5	10.0	6.0
26	8.0	3.2	11.0	6.0

SUMMARY OF OBSERVATIONS ON THE BATHYMETRIC
DISTRIBUTION OF FISH IN WISCONSIN LAKES

The data of the preceding sections lead to the following general conclusions. The depth of water inhabited by a single species of fish in the lakes of the Northeastern Highlands of Wisconsin varies rather widely from one lake to another; the relationship between size of fish and depth of water inhabited varies from lake to lake; different species that live at the same depths in one lake may inhabit different depths in another. The variations from lake to lake in the bathymetric distribution of fish exhibit no clear-cut dependence on differences in temperature and the concentrations of dissolved oxygen and free carbon dioxide.

Rock bass of all sizes exhibited a preference for the warm waters of the epilimnion in Muskellunge Lake, and so far as evidence is available appeared to select a similar shallow-water habitat in Trout Lake and Silver Lake (data for Clear Lake not adequate). In Nebish Lake, however, large rock bass were most abundant in the upper portion of the thermocline at depths about 2 to 4 meters greater than those occupied by small fish. Conditions with respect to temperature and the concentrations of oxygen and carbon dioxide do not seem to explain this peculiarity in the distribution of rock bass in Nebish Lake. Penetrations into the deeper regions of the lake, such as those made by the individual taken in Clear Lake at 15.5 meters and by the two rock bass captured at 11 meters in Muskellunge Lake, are rare.

The bathymetric distribution of the perch was variable from one lake to another. In Nebish Lake, and apparently in Trout Lake and Silver Lake also, perch of all sizes inhabited shallow water at about 3 to 5 meters (probably a little deeper at 5 to 7 meters in Silver Lake). The depth of greatest abundance of perch corresponds rather well with that of rock bass (except the large Nebish Lake rock bass) in all three lakes. An entirely different situation exists in Muskellunge Lake. Here the small perch exhibited a marked preference for the deepest, coldest strata that contained sufficient dissolved oxygen to support life. Among the four smaller mesh sizes, each increase in mesh size was accompanied by a 2-meter decrease in the depth at which the best catches were made. Large perch were taken most abun-

dantly at 5 to 7 meters—in shallow water but still below the depth of the greatest abundance of rock bass. The reason for the deep-water habitat of the smaller Muskellunge Lake perch is obscure. The small perch avoided these same depths in Silver Lake in spite of more suitable oxygen conditions. The somewhat lower temperatures of Silver Lake, as mentioned previously (p. 178), do not seem to account satisfactorily for the avoidance of the deeper water by small perch since the small perch of Muskellunge Lake appeared to seek out the coldest strata available. The capture of five perch in the hypolimnion of Clear Lake indicates an occasional penetration of deep water by perch in that body of water.

In Muskellunge Lake suckers were most abundant near the lower limit of the epilimnion and in the upper part of the thermocline. The larger mesh nets took their best catches 2 meters deeper (at 9 meters) than the smaller mesh nets (best catches at 7 meters). The Trout Lake data indicate a similar relationship between the size of suckers and the depths of water in which they are most numerous. In general, however, suckers were taken in shallower water in Trout Lake than in Muskellunge Lake. Suckers were taken in Silver Lake down to 7 meters, but were absent from the deep-water lifts.

Of all species for which data were obtained, the smallmouth black bass occurred most consistently in shallow water. This species appears to be almost exclusively an inhabitant of the epilimnion.

Wall-eyed pike were taken only in Clear Lake, Trout Lake, and Muskellunge Lake. In Clear Lake wall-eyed pike were taken throughout the hypolimnion as well as in the single shallow-water lift. In Muskellunge Lake all of the four wall-eyed pike captured were taken in less than 7 meters of water (see footnote to Table 11). The best catches of wall-eyed pike were made at 7 meters in Trout Lake but only one individual was taken below that depth and none were captured in the hypolimnion. Conditions with respect to water temperature and the concentrations of dissolved oxygen and free carbon dioxide are so similar in Trout Lake and Clear Lake that they cannot explain the differences in the distribution of the wall-eyed pike in the two lakes.

The bathymetric distribution of the cisco in Trout Lake, Muskellunge Lake, Silver Lake, and Clear Lake was described in some detail in an earlier publication (Hile, 1936). The summer distribution of the cisco, contrary to the other species studied, appears to depend closely on temperature and the concentration of dissolved oxygen. Aside from the occasional movement of a limited number of individuals into shallower water (or their failure to enter deep water), the cisco normally inhabits the coldest strata that contain sufficient oxygen to support life.

The belief that the bathymetric distribution of the cisco is correlated closely with temperature and the concentration of dissolved gases is supported by Fry's (1937) detailed study of the summer migrations of the cisco in Lake Nipissing, Ontario. With the warming of the epilimnion in late spring and early summer the ciscoes move downward—most of them below the thermocline where they scatter throughout the hypolimnion. Later in the season (late August and September) as the oxygen concentration in deep water diminishes and the concentration of free carbon dioxide increases they become concentrated immediately below the thermocline. Before the autumn turnover most of them return to the shallow water of the epilimnion. Fry considered the increase in free carbon dioxide in deep water more significant than the decrease in dissolved oxygen as the cause of the concentration of ciscoes below the thermocline in late August and September.

The data on the bathymetric distribution of other species that occur in these northeastern Wisconsin lakes are too scanty to warrant treatment in this summary.

Certain of the conclusions as to the variability of the bathymetric distribution of fishes find support in the observations of Pearse (1921a)¹¹ on the distribution of fish in other Wisconsin lakes. Since Pearse's fishing operations were carried out be-

¹¹ In this publication Pearse presented original data on the distribution of fish in three lakes, Lake Michigan (near Sturgeon Bay, Wisconsin), Lake Pepin, and Lake Geneva, and summarized earlier findings on Lake Wingra and Lake Mendota (Pearse and Achtenberg, 1920) and Green Lake (Pearse, 1921b). The data for Lake Pepin, an expansion of the Mississippi River are not comparable with those for glacial lakes. In Lake Wingra, whose maximum depth is only 4.3 meters, the bathymetric distribution of fish is not an important problem.

tween late June and early September, his data are comparable to those of the present investigation. In each of four lakes rock bass were most abundant at 5 to 10 meters (Lake Michigan, Lake Geneva) or were equally plentiful at 0 to 5 and at 5 to 10 meters (Green Lake, Lake Mendota). The 5- to 10-meter stratum marked the lower limit of occurrence of rock bass in Lake Michigan, Green Lake and Lake Mendota, but in Lake Geneva this species ranged down to the depth of 15 to 20 meters. Small-mouth black bass were taken as deep as 20 to 25 meters in Lake Geneva as compared with a maximum of 10 to 15 meters in Green Lake. Wall-eyed pike also were present in relatively deep water (as deep as 15 to 20 meters) in Lake Geneva. In Lake Mendota wall-eyed pike were taken only in the 0- to 5-meter stratum.

Perch were present in the greatest depths that oxygen conditions permitted in both Lake Mendota (greatest depth of occurrence—10 to 15 meters) and Lake Geneva (greatest depth of occurrence—30 to 35 meters) and even penetrated the oxygenless regions of the former lake. The greatest depth at which perch were taken in Lake Geneva exceeded even the maximum depth of occurrence of ciscoes (20 to 25 meters). In Lake Mendota, however, neither species was present below 15 meters. The association of perch and ciscoes in Lake Geneva and Lake Mendota is in contrast to the situation in Green Lake, where no ciscoes were captured in water less than 40 meters deep, while perch were taken only in the 5- to 10-meter stratum. Perch were captured in Lake Michigan at 25 to 30 meters, the greatest depth at which experimental gill nets were set. They were much more abundant, however, in shallower water (best catches at 5 to 10 meters).

The maximum depth of occurrence of common suckers varied from 5 to 10 meters in Lake Mendota to 10 to 15 meters in Lake Geneva and Green Lake and 15 to 20 meters in Lake Michigan.

Pearse's observations confirm the statement made previously (p. 181) that the relationship between the bathymetric distribution of fish in lakes and the conditions with respect to temperature and dissolved gases (especially oxygen) is not clear-cut. The perch provides an outstanding example of the looseness of this relationship. In some lakes (Geneva, Mendota, and Muskel-

lunge) perch appear to select the coldest water containing sufficient oxygen to support life, and may even penetrate strata in which the oxygen is deficient or lacking (Mendota, Muskellunge?). Under these conditions the perch is an associate of the typically cold-water form, the cisco. In other lakes (Silver, Trout, and Green) the perch exhibits a marked preference for shallow water in spite of an abundance of cold, well-oxygenated water in the thermocline and hypolimnion.

The perch shows also a wide variation in the relationship between the size of fish and the depth of water inhabited. Individuals of all sizes lived at approximately the same depths in Nebish, Trout, Silver, Geneva, and Mendota.¹² In Muskellunge Lake, however, the progressively larger perch inhabited the progressively shallower strata. As an example of a situation that is the reverse of the one found in Muskellunge Lake may be cited the bathymetric distribution of perch in Lake Wawasee in northern Indiana.¹³ During the summer small perch were taken in large numbers in the weedy areas of the shallow water, but large individuals were taken only in deep water where they were captured by hook and line just above the bottom at a depth of approximately 40 feet or 12 meters.

The data of the preceding pages contain similar, if less striking, examples in which the bathymetric distribution of other species varied among lakes that were apparently closely similar, or in which the distribution failed to exhibit a close dependence on temperature and oxygen conditions. It is true that the cisco appears invariably to seek the coldest water that contains sufficient oxygen to support life.¹⁴ Even this selection may be a matter of preference rather than necessity for it has been demonstrated that the cisco, which was formerly considered strictly a stenothermal species limited in its occurrence to the colder strata of the deeper lakes, can tolerate very high temperatures (Scott, 1931; Hile, 1936).

¹² This statement, as it refers to Lake Geneva and Lake Mendota, is based on the examination of the average catches of gill nets of different sizes of mesh.

¹³ Statements relative to the bathymetric distribution of fish in Lake Wawasee are based on personal observations made by Hile in the summers of 1926, 1927, and 1928.

¹⁴ This statement applies only to the smaller inland lakes. The Great Lakes herring is typically a shallow-water form, although it does move offshore to somewhat deeper water during the hot summer months.

The failure to correlate closely the bathymetric distribution of certain species with temperature and oxygen conditions should not be taken as an indication that these two factors are unimportant in the determination of the depth of water at which fish live. Certainly a lack of oxygen constitutes a complete barrier to long-time occupancy. Furthermore, the existence of temperature preference is too well established for even conspicuous exceptions to throw doubt on the general importance of temperature as a factor in distribution. Nevertheless, it is apparent that the modifying or interfering effects of local conditions may go far toward obscuring the influence of temperature and oxygen conditions. The precise nature of these "local factors" is to a large extent a matter for speculation. Obviously, however, they exert sufficient influence to make the ecological aspect of the bathymetric distribution of fish a very complex problem and to show the importance of the recognition of pronounced "individualities" in lakes and their fish population.

Among the more important factors in addition to temperature and oxygen conditions that may be expected to affect the bathymetric distribution of fish are: hereditary physiological differences among stocks of the same species and resultant variation in the reactions to environmental conditions; distribution of food as to kind and quantity; the abundance of fish of the same and other species; configuration of the lake basin and the topography of the surrounding land-especially as related to wind and wave action; the type of bottom as it affects the abundance of bottom organisms and rooted plants; the abundance and distribution of larger aquatic plants as sources of food and shelter. These potential factors have many interrelationships. A discussion of these interrelationships is beyond the scope of this paper. However, a listing of certain probable contributing factors does serve to emphasize the fact that no simple explanation of variations in the bathymetric distribution of fish in lakes is to be expected.

LITERATURE CITED

- Couey, Faye M. 1935. Fish food studies of a number of northeastern Wisconsin lakes. *Trans. Wis. Acad. Sci., Arts and Let.* 29: 131-172.
- Fry, F. E. J. 1937. The summer migration of the cisco, *Leucichthys artedii* (Le Sueur), in Lake Nipissing, Ontario. *Univ. Toronto Studies, Biol. Ser. No. 44, Pubs. Ontario Fish. Res. Lab.* LV: 91 pp.

- Hile, Ralph. 1936. Age and growth of the cisco, *Leucichthys artedi* (Le Sueur), in the lakes of the northeastern highlands, Wisconsin. Bul. Bur. Fish. 48: 211-317.
- Pearse, A. S. 1921a. The distribution and food of the fishes of three Wisconsin lakes in summer. University of Wisconsin Studies in Science, No. 3, 61 pp.
- Pearse, A. S. 1921b. Distribution and food of the fishes of Green Lake, Wisconsin, in summer. Bul. Bur. Fish. 37: 254-272.
- Pearse, A. S. and Henrietta Achtenberg. 1920. Habits of yellow perch in Wisconsin lakes. Bul. Bur. Fish. 36: 297-366.
- Powers, Edwin B. 1938. Factors involved in the sudden mortality of fishes. Trans. Amer. Fish. Soc. 67: 271-281.
- Powers, E. B., Howard H. Rostorfer, Lula Mae Shipe, and Theresa Hickman Rostorfer. 1938. The relation of respiration of fishes to environment. XII. Carbon dioxide tension as a factor in various physiological respiratory responses in certain fresh water fishes. Jour. Tenn. Acad. Sci. 13(3): 220-245.
- Schneberger, Edward. 1935. Growth of the yellow perch (*Perca flavescens* Mitchill) in Nebish, Silver and Weber lakes, Vilas County, Wisconsin. Trans. Wis. Acad. Sci., Arts and Let. 29: 103-130.
- Scott, Will. 1931. The lakes of northwestern Indiana. Investigations of Indiana lakes. No. III. Department of Conservation, State of Indiana. Publication No. 107: 57-145.
- Shelford, Victor E. and W. C. Allee. 1913. The reactions of fishes to gradients of dissolved atmospheric gases. Jour. Exper. Zool. 14 (2): 207-266.
- Smith, Frank. 1924. Variation in the maximum depth at which fish can live during summer in a moderately deep lake with a thermocline. Bul. Bur. Fish. 41: 1-7.
- Spoor, William A. and Clarence L. Schloemer. 1939. Diurnal activity of the common sucker, *Catostomus commersonnii* (Lacépède), and the rock bass, *Ambloplites rupestris* (Rafinesque), in Muskellunge Lake. Trans. Amer. Fish. Soc. 68: 211-220.
- Wilding, James L. 1939. The oxygen threshold for three species of fish. Ecology 20: 253-263.

GROWTH OF THE ROCK BASS, *AMBLOPLITES RUPESTRIS* (*RAFINESQUE*), IN FIVE LAKES OF NORTH- EASTERN WISCONSIN

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ABSTRACT

The forms of the growth curves of rock bass from four lakes in northeastern Wisconsin with medium-hard to hard water bore a general resemblance to each other, but differed sharply from the curve for rock bass from a lake with extremely soft water. With the exception of a slight increase in growth in the third year of life the annual increments of length of the rock bass of Nebish Lake (4.0 p.p.m. of bound CO₂) tended to decrease consistently beyond the first year. The good first-year growth in length of rock bass of Allequash, Silver, and Trout Lakes (16.8, 15.0, and 18.7 p.p.m., respectively, of bound CO₂) was followed by poor growth in the second, third, and fourth years of life. This poor growth was followed in turn by good growth in the fifth and sixth years. The annual increments of length tended to decline beyond the sixth year of life. The growth of rock bass of Muskellunge Lake (10.0 p.p.m. of bound CO₂) declined sharply in the second year of life. The annual increments of length were fairly constant in the second to seventh years, inclusive, but declined beyond the seventh year. In each lake the males grew more rapidly than the females.

The time of attainment of the legal total length of 7 inches in the different lakes ranged from late in the sixth growing season in Nebish and Trout Lakes to the middle of the eighth growing season in Muskellunge Lake.

Rock bass of corresponding length from Allequash, Silver, and Trout Lakes were so nearly of the same weight that one curve described the length-weight relationship of the three stocks. Muskellunge Lake rock bass were considerably lighter than fish of the same length from these three lakes, and Nebish Lake rock bass were somewhat lighter than those from Muskellunge Lake.

INTRODUCTION

Increasing recognition is being given to the importance of studies of growth rate in connection with fishery management. It has been stated repeatedly that the rate of growth reflects the suitability of a lake or stream for a particular species, and that sound management, especially stocking programs, cannot be developed without a knowledge of the growth rate of fish in different waters. If growth is slow, it is said, food is scarce or the fish are overcrowded and no stocking of that species should be made. On the other hand, fish may be stocked in waters where growth is good.

In actual practice, applications of growth-rate studies to fishery management have not been widespread. For many of our game fishes and panfishes the available information on growth rate is so scanty that we are without proper standards from which to judge whether the growth observed in a particular locality is to be considered

good or poor. The effective use of growth-rate studies as a tool of fishery management will require sufficiently extensive data on the variations of growth rates of important species in different waters to permit the accurate evaluation of the quality of growth in any single locality. These necessary data can be accumulated but slowly and through the combined efforts of numerous investigators.

The present paper is a contribution to the available information on the growth of the rock bass in the lakes of the northeastern highlands of Wisconsin. Although the collections of rock bass from Allequash, Silver, and Trout Lakes were small, it is believed that the general growth curves based on them are reasonably dependable, and that these curves, together with data on the growth of the rock bass of Muskellunge Lake and Nebish Lake, provide a fair idea of the general rate of growth of rock bass and of the variations in growth rate to be expected in the lakes of that region. The data on the growth of the Nebish Lake rock bass have been taken from a paper by Hile (1941).

Limnological data¹ (Table 1) reveal considerable differences among the five lakes. In size they range from Nebish Lake with a surface area of only 38.5 hectares (95 acres) to Trout Lake with an area of 1,583 hectares (3,912 acres). The maximum depths range from 7.5 meters (25 feet) in Allequash Lake to 35.0 meters (115 feet) in Trout Lake. For lakes of this region the waters of Trout, Allequash, Silver, and Muskellunge Lakes may be termed medium hard to hard. Nebish Lake has extremely soft water. The organic matter of the plankton is greater in Allequash Lake than in any one of the other four. This high production of plankton is associated with relatively low transparency (only 1.5 meters).

An earlier study of the growth of rock bass in Trout and Muskellunge Lakes was made by Wright (1929). His data will not be compared with those of the present study since he had no individual sex records and employed a method for the computation of growth histories from scale measurements different from the one used here.

Table 1.—Limnological data concerning five lakes of the northeastern highland district, Wisconsin

[The data on bound CO₂ and organic matter of the plankton refer to average surface conditions.]

Lake	Area (hectares)	Maximum depth (meters)	Average depth (meters)	Secchi disk transparency (meters)	Bound CO ₂ (p.p.m.)	Organic matter of plankton (p.p.m.)
Allequash	142	7.5		1.5	16.8	1.48
Muskellunge	372.3	21.0	7.0	4.0	10.0	1.16
Nebish	38.5	15.8	5.2	6.0	4.0	0.77
Silver	87.3	19.5	11.3	5.5	15.0	0.85
Trout..... {North Basin	533	31.0	12.9	5.0	18.5	0.66
{South Basin	1,050	35.0	14.2	4.5	18.7	0.92

¹The data of Table 1 were made available through the courtesy of Dr. Chancey Juday of the Wisconsin Geological and Natural History Survey.

MATERIALS AND METHODS

The months and years of capture of the rock bass employed for the study of age and growth were: Allequash Lake—August, 1930 (20 fish); Muskellunge Lake—July, August, and September, 1930-1932 (533 fish); Silver Lake—July and August, 1930 and 1931 (154 fish); Trout Lake—July, August, and September, 1930 (77 fish). For data on materials from Nebish Lake see Hile (1941). The collections were taken by gill nets and by hook-and-line fishing. In order to minimize selection, gill nets of four to seven different mesh sizes were included in each set and only small hooks were employed in fishing by hook and line. Even so, the data for certain of the younger age groups were excluded as not representative. Only those age groups for which complete records of sex were available were employed in the study of growth.

Lengths and weights of fish for which records of sex were lacking, and the use of data from certain additional collections taken in 1928, 1931, and 1932 made available a total of 941 specimens for the study of the length-weight relationship of rock bass from Allequash, Silver, and Trout Lakes, and 1,646 specimens for the study of the length-weight relationship of the Muskellunge Lake rock bass.

Scales for the investigation of growth were mounted on glass slides and examined and measured with the aid of a microprojection apparatus. Details as to the method of measuring the scales and calculating the growth from scale measurements were given by Hile (1941). It was assumed that the method of calculating growth, established empirically from a study of the body-scale relationship of rock bass from Muskellunge and Nebish Lakes, was applicable to the data on rock bass from Allequash, Silver, and Trout Lakes.

GROWTH IN LENGTH AND WEIGHT

Only general growth curves will be presented since, with the exception of the Muskellunge Lake and Silver Lake collections, the numbers of fish were so small that the data for the individual age groups could not be considered dependable. (Data on the age and year-class composition of samples of rock bass from Muskellunge and Silver Lakes and on annual fluctuations in the growth of certain year classes of rock bass in those lakes were included by Hile (1941) in a study of factors affecting the growth and abundance of rock bass in the lakes of northeastern Wisconsin.) In general, the lengths in Table 2 are grand average calculated lengths, although the successive addition of grand average increments of calculated length was employed to determine the lengths in the later years of life. The use of average increments effects a natural smoothing of the growth curves. The growth curves as determined from a combination of the data for the sexes are presented in Figure 1.² The vertical scales of the figure are given

²I am indebted greatly to Dr. Frank W. Jobes who prepared the figures for this paper.

Table 2.—*Calculated standard lengths at the end of each year of life of rock bass from five lakes of northeastern Wisconsin*
 [Number of specimens indicated in parentheses]

Lake	Sex	Calculated length in millimeters at end of year of life										
		1	2	3	4	5	6	7	8	9	10	11
Allequash	Male	37 (11)	58 (11)	75 (11)	94 (11)	117 (11)	139 (8)	152 (6)	163 (2)	...	...	...
	Female	36 (9)	52 (9)	69 (9)	88 (9)	110 (8)	128 (6)	142 (4)	150 (1)	159 (1)	165 (1)	...
	Both	36	55	72	91	114	134	147	156	...	...	...
Muskellunge	Male	33 (220)	51 (220)	69 (220)	88 (208)	107 (190)	124 (166)	142 (138)	157 (103)	172 (38)	180 (9)	186 (1)
	Female	33 (313)	51 (313)	68 (313)	86 (300)	103 (272)	119 (244)	135 (199)	147 (162)	160 (69)	170 (25)	179 (3)
	Both	33	51	68	87	105	122	138	152	166	175	182
Nebish	Male	35 (395)	62 (395)	92 (395)	119 (346)	139 (322)	153 (269)	163 (254)	171 (207)	177 (79)	184 (18)	191 (3)
	Female	34 (586)	62 (586)	90 (586)	113 (519)	130 (488)	142 (430)	150 (396)	156 (220)	162 (195)	168 (72)	174 (21)
	Both	34	62	91	116	134	147	156	163	169	176	182
Silver	Male	31 (59)	48 (59)	70 (59)	88 (41)	118 (37)	142 (8)	166 (3)	179 (2)	186 (2)	...	...
	Female	31 (95)	48 (69)	68 (95)	86 (95)	112 (69)	133 (31)	154 (9)	173 (4)	181 (3)	...	...
	Both	31	48	69	87	115	138	160	176	184	...	...
Trout	Male	32 (25)	50 (25)	70 (25)	93 (24)	123 (23)	153 (7)	171 (7)	186 (4)	195 (2)	...	...
	Female	32 (52)	52 (52)	72 (52)	93 (50)	119 (45)	141 (23)	154 (19)	168 (12)	177 (5)	183 (1)	...
	Both	32	51	71	93	121	147	162	177	186	...	...

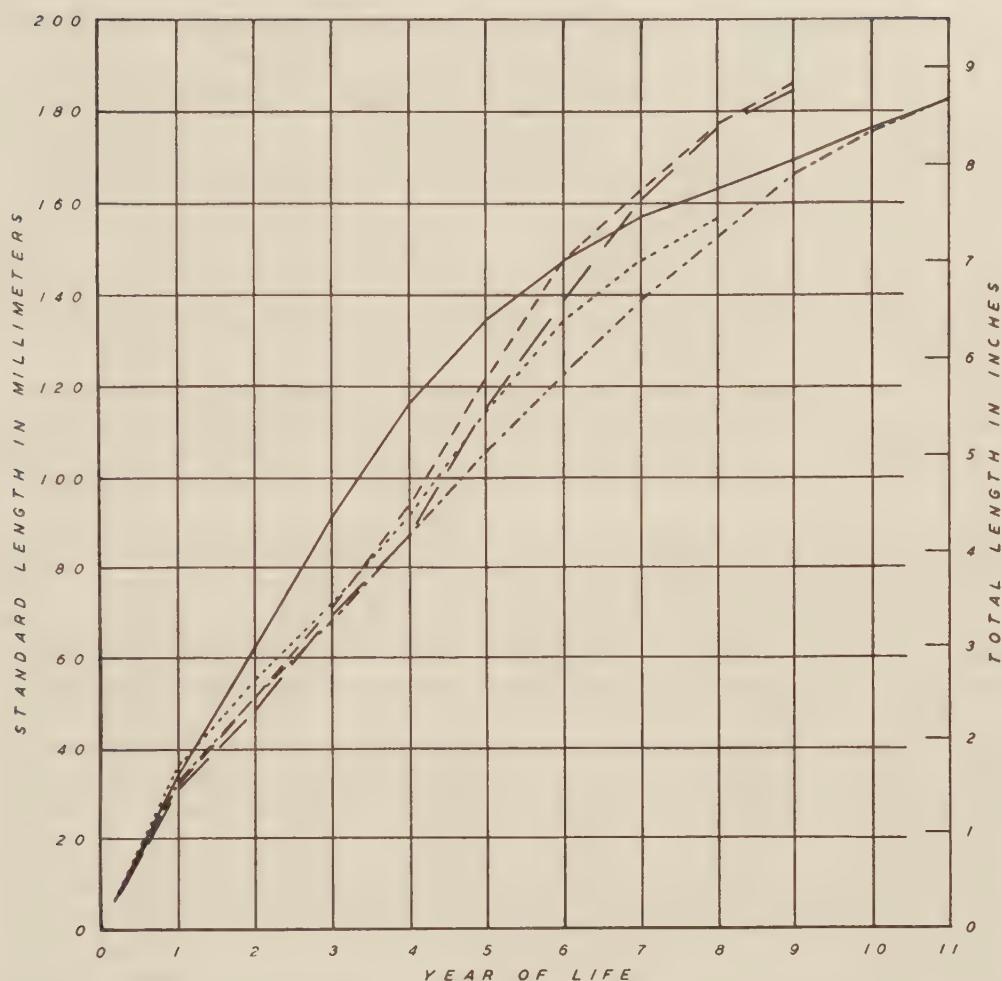


Figure 1.—Calculated growth in length (data for the sexes combined) of rock bass from Allequash Lake (dotted line), Muskellunge Lake (dots and dashes), Nebish Lake (solid line), Silver Lake (long dashes), and Trout Lake (short dashes)

in terms of both standard length in millimeters and total length in inches.

Each stock of rock bass was characterized by sex differences in growth rate, with the males showing the more rapid growth in the later years of life. This condition appears to be characteristic of centrarchids. The age at which a sex difference in length was clearly established varied in the different populations. The earliest years of life, by the end of which the males averaged 5 millimeters or more longer than the females, were: Allequash Lake—second year of life (very few specimens); Muskellunge Lake—sixth year; Nebish Lake—fourth year; Silver Lake—fifth year; Trout Lake—sixth year. The maximum difference between the calculated lengths of males and females in corresponding years of life ranged from 12 millimeters in Muskellunge

Table 3.—Calculated increments of standard length in each year of life of rock bass from five lakes of northeastern Wisconsin

Lake	Sex	Calculated increment of length in millimeters in year of life										
		1	2	3	4	5	6	7	8	9	10	11
Allequash	Male	37	21	17	19	23	22	13	11			
	Female	36	16	17	19	22	18	14	8	9	6	
	Both	36	19	17	19	23	20	13	9			
Muskellunge	Male	33	18	18	19	19	17	18	15	15	8	6
	Female	33	18	17	18	17	16	16	12	13	10	9
	Both	33	18	17	19	18	17	16	14	14	9	7
Nebish	Male	35	27	30	27	20	14	10	8	6	7	7
	Female	34	28	28	23	17	12	8	6	6	6	6
	Both	34	28	29	25	18	13	9	7	6	7	6
Silver	Male	31	17	22	18	30	24	24	13	7		
	Female	31	17	20	18	26	21	21	19	8		
	Both	31	17	21	18	28	23	22	16	8		
Trout	Male	32	18	20	23	30	30	18	15	9		
	Female	32	20	20	21	26	22	13	14	9	6	
	Both	32	19	20	22	28	26	15	15	9		

Lake (end of ninth year) and Silver Lake (end of seventh year) to 18 millimeters in Trout Lake (end of eighth and ninth years).

The general growth curves (Tables 2 and 3, Fig. 1) reveal a pronounced difference in the growth of Nebish Lake rock bass as compared with the growth of rock bass from the other lakes. The length increments (Table 3) of the Nebish Lake rock bass were large in the early years of life and with the exception of the third year decreased consistently with increase of age up to the eighth or ninth year, beyond which point the increments tended to remain constant. In Allequash, Silver, and Trout Lakes the first-year growth of 31 to 37 millimeters (the actual growth varied with lake and sex) was followed by relatively poor growth in the second, third, and fourth years. This slow growth was followed in turn by a secondary period of rapid growth in the fifth and sixth years (continued into the seventh year of life of the Silver Lake fish). The only exception to this trend was provided by the sixth-year increment of Allequash Lake females. Beyond the sixth or seventh year the growth increments of rock bass from these three lakes tended to decrease with increase in age. The growth increments of the Muskellunge Lake rock bass decreased sharply in the second year and thereafter exhibited only unimportant fluctuations (maximum of 2 millimeters in each sex) up to the end of the seventh year of life. The length increments tended to decrease beyond the seventh year. The growth of the Muskellunge Lake rock bass differed from the growth of rock bass in Allequash, Silver, and Trout Lakes chiefly in the absence of the secondary period of rapid growth.

Because of the differences in the style of growth the Nebish Lake rock bass had greater calculated lengths than the rock bass from the other four lakes in the second to sixth years of life inclusive. (The sixth-year length of male rock bass from Trout Lake provides a single exception.) The advantage of the Nebish Lake fish increased from the second to the fourth year, but with the exception of the Muskel-

lunge Lake rock bass in the fifth year, the Nebish Lake fish had the lowest annual increments of length in the fifth to ninth years, inclusive. The Trout Lake rock bass had practically overtaken the Nebish Lake fish by the end of the sixth year and had distinctly the higher calculated lengths beyond the sixth year. Similarly, Silver Lake rock bass were longer than Nebish Lake fish in the seventh and later years of life. The length of the Muskellunge Lake females first surpassed that of the Nebish Lake females in the tenth year; this advantage was increased slightly in the eleventh year. However, the Muskellunge Lake males did not overtake the Nebish Lake males, although they reduced the advantage of the Nebish Lake fish substantially. The data for the Allequash Lake rock bass must be recognized as inadequate. The available information indicates the Nebish Lake rock bass to have been consistently longer than Allequash Lake fish of corresponding age throughout the later years of life.

From the standpoint of conservation the course of growth during the early years of life may not be of particularly great significance. It is more important to know the age at which legal length is attained and the relationship of age to size among fish above legal length. In the inland lakes of Wisconsin the size limit for rock bass is 7 inches, total length (146 millimeters, standard length). This length was attained by the rock bass from Nebish Lake and Trout Lake toward the end of the sixth growing season, by the Silver Lake rock bass in the first half of the seventh growing season, by the Allequash Lake rock bass toward the close of the seventh growing season, and by the Muskellunge Lake rock bass near the middle of the eighth growing season. Actually, the males of each lake required somewhat less time and females somewhat more time than indicated in the preceding sentence to reach legal size. The data of Table 2 suggest that males attain legal length about a year sooner than females (less than a year in some lakes; more than a year in others).

If attention is confined to fish above legal length, the Nebish Lake rock bass, in spite of its rapid growth in early years, must be classified as a stock with poorer growth than was found in Silver Lake and Trout Lake.

The calculated weights of Table 4 (see also Table 5 and Fig. 2), which correspond to the calculated lengths of Table 2, were computed by means of the length-weight equations given in the next section of this paper. The fact that the Nebish Lake rock bass weighed less than fish of corresponding length from the other four lakes places the growth of the Nebish Lake rock bass in a less favorable light when growth is expressed in terms of weight rather than length. Similarly the slow growth of the Muskellunge Lake rock bass is accentuated by the fact that fish from that lake had lower average weights than fish of the same length from Allequash, Silver, and Trout Lakes. The calculated weights of the Nebish Lake rock bass were greater than those of rock bass from the other four lakes in the second to fifth years,

Table 4.—Calculated weights (corresponding to the calculated lengths of Table 2) at the end of each year of life of rock bass from five lakes of northeastern Wisconsin

Lake	Sex	Calculated weight in grams at end of year of life										
		1	2	3	4	5	6	7	8	9	10	11
Allequash	Male	2	7	14	29	56	95	125	154			
	Female	2	5	11	23	46	74	101	120	143	160	
	Both	2	6	12	26	51	84	113	137			
Muskellunge	Male	1	4	10	21	38	59	88	119	157	179	198
	Female	1	4	10	20	34	52	76	98	126	151	176
	Both	1	4	10	20	36	56	82	108	141	165	187
Nebish	Male	1	7	23	49	79	105	127	146	162	182	204
	Female	1	7	21	42	64	84	99	111	124	139	154
	Both	1	7	22	46	72	95	113	128	143	160	179
Silver	Male	1	4	12	23	57	101	163	205	231		
	Female	1	4	11	22	49	83	130	185	212		
	Both	1	4	11	22	53	92	146	195	222		
Trout	Male	1	4	12	28	65	127	178	231	267		
	Female	1	5	13	28	59	99	130	169	198	220	
	Both	1	4	12	28	62	113	154	200	232		

inclusive, with the single exception of the Allequash males at the end of the second year. At the end of the sixth year the Nebish Lake fish weighed less than rock bass from Trout Lake and were only slightly heavier than Silver Lake fish. At the end of the seventh year of life Trout Lake and Silver Lake rock bass of both sexes and the Allequash Lake females weighed more than the Nebish Lake fish, and in the eighth and later years Nebish Lake rock bass were consistently lighter than fish of corresponding age from the former three lakes. Attention is called particularly to the large increments of weight of the Silver Lake and Trout Lake rock bass in the sixth to eighth years of life. The unweighted means for the sexes show that at the end of the ninth year Nebish Lake fish weighed only a little more than 5 ounces, as compared with a weight of about 8 ounces for rock bass from Silver and Trout Lakes. With increase in age the Muskellunge Lake males reduced substantially the advantage of the Nebish Lake males but remained the lighter in all the later years of life. The females from Muskellunge

Table 5.—Calculated increments of weight in each year of life of rock bass from five lakes of northeastern Wisconsin

Lake	Sex	Calculated increment of weight in grams in year of life										
		1	2	3	4	5	6	7	8	9	10	11
Allequash	Male	2	5	7	15	27	39	30	29			
	Female	2	3	6	12	23	28	27	19	23	17	
	Both	2	4	6	14	25	33	29	24			
Muskellunge	Male	1	3	6	11	17	21	29	31	38	22	19
	Female	1	3	6	10	14	18	24	22	28	25	25
	Both	1	3	6	10	16	20	26	26	33	24	22
Nebish	Male	1	6	16	26	30	26	22	19	16	20	22
	Female	1	6	14	21	22	20	15	12	13	15	15
	Both	1	6	15	24	26	23	18	15	15	17	19
Silver	Male	1	3	8	11	34	44	62	42	26		
	Female	1	3	7	11	27	34	47	55	27		
	Both	1	3	7	11	31	39	54	49	27		
Trout	Male	1	3	8	16	37	62	51	53	36		
	Female	1	4	8	15	31	40	31	39	29	22	
	Both	1	3	8	16	34	51	41	46	32		

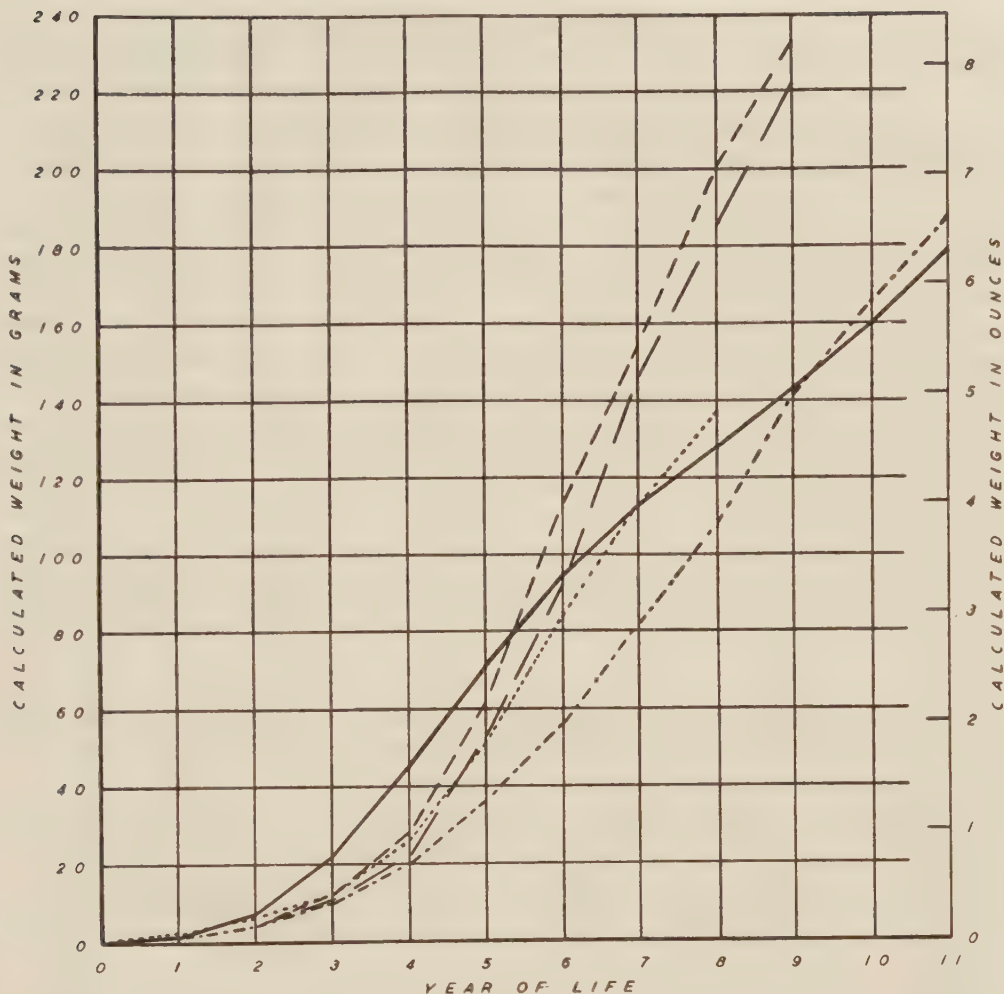


Figure 2.—Calculated growth in weight (data for the sexes combined) of rock bass from Allequash Lake (dotted line), Muskellunge Lake (dots and dashes), Nebish Lake (solid line), Silver Lake (long dashes), and Trout Lake (short dashes)

Lake, however, weighed more than females from Nebish Lake in the ninth, tenth, and eleventh years of life.

For the present, the problem of the factors contributing to the observed differences in the growth of the rock bass in the various lakes must remain unanswered. Possibly some significance may be attached to the fact that the general growth curves of the rock bass from lakes with medium-hard to hard water (especially Allequash, Silver, and Trout Lakes) were in general similar, but differed sharply from the growth curve of the rock bass from the soft water of Nebish Lake.

LENGTH-WEIGHT RELATIONSHIP

The preliminary tabulations of the data on the length-weight relationship of the rock bass from Allequash, Silver, and Trout Lakes in-

cluded a division of the material according to lake, sex (records of sex were not available for all collections), and year and month of capture. Since no large or consistent differences were found among the several groups, all available materials were combined for the preparation of Table 6. The length-weight data of this table may be considered descriptive of rock bass of all three populations. Preliminary tabulations of the length-weight data for the Muskellunge Lake rock bass justified the combination of the data for the sexes and the combination of collections taken in different months and years, with the exception of a sample of 89 fish taken during the first 17 days of August, 1935. The rock bass of this collection were so much heavier in relation to their length than were fish taken in earlier years that they were excluded in the preparation of Table 7. A similar situation was found in Nebish Lake by Hile (1941), who observed that rock bass taken from that body in 1935 were in far better condition than fish collected in 1930-1932.

In Figure 3 the dots indicate the actual average weights of Allequash Lake, Silver Lake, and Trout Lake rock bass within 5-millimeter intervals of length; the open circles give the corresponding data

Table 6.—Length-weight relationship of rock bass as determined from the combined collections from Allequash, Silver, and Trout Lakes

Standard length (millimeters)	Weight (grams)		Total length (inches)	Weight (ounces)	Number of fish
	Actual	Calculated			
217	374	370	10.4	13.2	1
212	415	344	10.1	14.6	1
207	334	320	9.9	11.8	1
202	288	297	9.6	10.2	5
197	274	275	9.4	9.7	7
192	247	254	9.2	8.7	13
187	226	235	8.9	8.0	10
182	220	216	8.7	7.8	10
177	202	198	8.4	7.1	11
172	184	182	8.2	6.5	20
167	171	166	8.0	6.0	17
162	154	151	7.7	5.4	26
157	147	137	7.5	5.2	19
152	122	125	7.3	4.3	20
147	115	112	7.0	4.1	30
142	101	101	6.8	3.6	34
137	88	91	6.6	3.1	41
132	81	81	6.3	2.9	61
127	71	72	6.1	2.5	68
122	65	64	5.8	2.3	51
117	56	56	5.6	2.0	53
112	49	49	5.4	1.7	73
107	43	43	5.1	1.5	53
102	35	37	4.9	1.2	39
97	31	32	4.7	1.1	27
92	28	27	4.4	1.0	27
87	22	23	4.2	0.8	18
82	18	19	3.9	0.6	37
77	16	16	3.7	0.5	35
72	12	13	3.5	0.4	20
67	11	10	3.2	0.4	9
62	8	8	3.0	0.3	4

¹Actual value is 0.56.

Table 7.—Length-weight relationship of the Muskellunge Lake rock bass as determined from the combined collections of 1928 and 1930-1932

Standard length (millimeters)	Weight (grams)		Total length (inches)	Weight (ounces)	Number of fish
	Actual	Calculated			
207	267	272	9.9	9.4	3
202	259	253	9.6	9.1	8
197	239	235	9.4	8.4	8
192	224	218	9.2	7.9	12
187	205	201	8.9	7.2	22
182	191	185	8.7	6.7	34
177	172	171	8.4	6.1	48
172	159	157	8.2	5.6	48
167	145	143	8.0	5.1	37
162	129	131	7.7	4.6	54
157	117	119	7.5	4.1	77
152	107	108	7.3	3.8	78
147	97	98	7.0	3.4	78
142	87	88	6.8	3.1	82
137	80	79	6.6	2.8	68
132	72	71	6.3	2.5	59
127	62	63	6.1	2.2	40
122	54	56	5.8	1.9	58
117	49	50	5.6	1.7	51
112	43	43	5.4	1.5	43
107	36	38	5.1	1.3	52
102	32	33	4.9	1.1	91
97	28	28	4.7	1.0	92
92	23	24	4.4	0.8	89
87	20	20	4.2	0.7	148
82	17	17	3.9	0.6	124
77	15	14	3.7	0.5	64
72	11	12	3.5	0.4	55
67	11	9	3.2	0.4	19
62	6	7	3.0	0.2	2
57	..	6	2.7		..
52	4	4	2.5	0.1	1

for the Muskellunge Lake rock bass. The curves that follow through the two sets of points are solutions of the parabolas:

$$W = 2.667 \times 10^{-5} L^{3.057},$$

and
$$W = 3.307 \times 10^{-5} L^{2.986},$$

where W = weight in grams,

and L = standard length in millimeters.

The first of the above equations applies to the rock bass from Allequash, Silver, and Trout Lakes and the second to the Muskellunge Lake rock bass.

For comparison a curve showing the length-weight relationship of Nebish Lake rock bass taken in late July and early August of 1930-1932 has been included in Figure 3. This curve is a graph of the equation:

$$W = 2.884 \times 10^{-5} L^{3.003}$$

Complete tabular data on the length-weight relationship of the Nebish Lake rock bass may be found in a publication by Hile (1941).

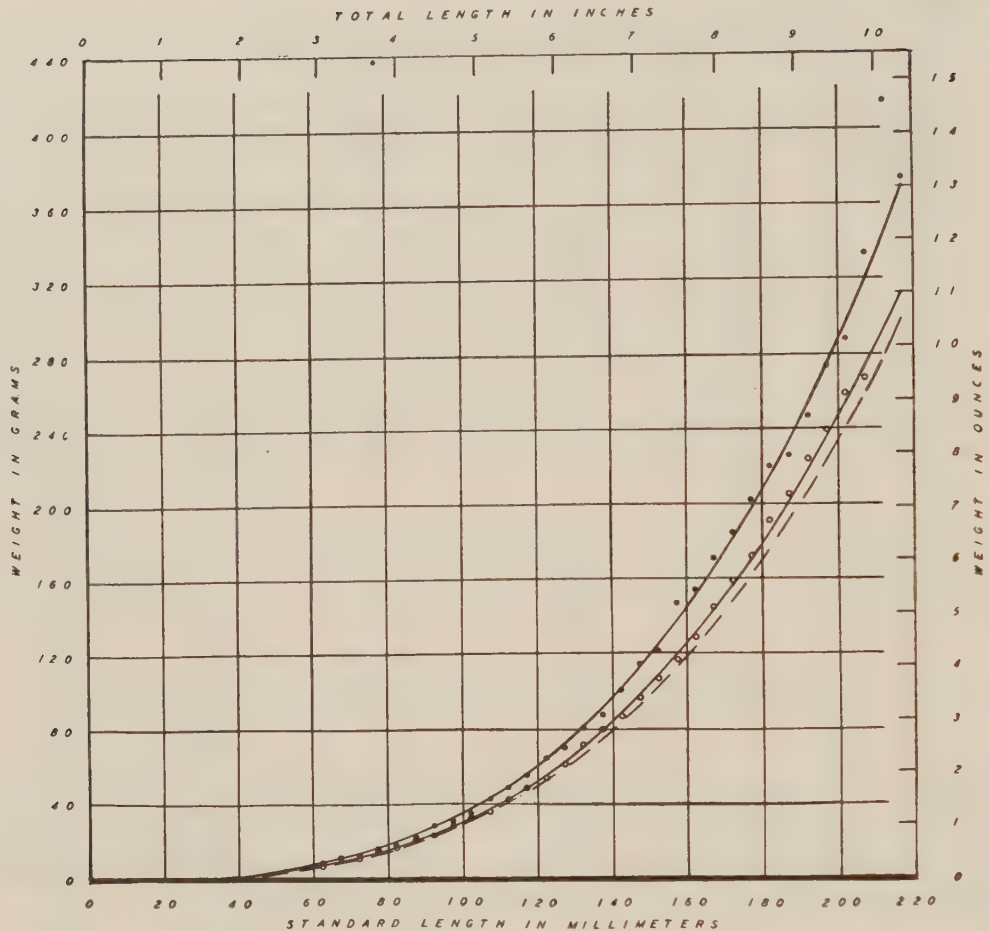


Figure 3.—Length-weight relationship of rock bass from Allequash, Silver, and Trout Lakes (dots) and Muskellunge Lake (open circles). The smooth curves passing through the two sets of points are graphs of the length-weight equation. The broken curve shows the length-weight relationship of the Nebish Lake rock bass (empirical data not plotted).

The relatively low weights of the Nebish Lake fish provide a ready explanation for the fact that the growth of the Nebish Lake rock bass appears less favorably in comparison with rock bass of the other lakes when growth is expressed in terms of weight instead of length. At the legal length of 7 inches the Nebish Lake rock bass weighed only 3.2 ounces as compared with 3.4 ounces for the Muskellunge Lake rock bass and 3.9 ounces for fish from Allequash, Silver, and Trout Lakes. At the length of 9 inches the weights of rock bass from the various lakes were: Nebish Lake, 7.0 ounces; Muskellunge Lake, 7.3 ounces; Allequash, Silver, and Trout Lakes, 8.6 ounces.

In the length-weight relationship as well as in the general form of the growth curves the rock bass from the lakes with medium-hard to

hard water differed from the Nebish Lake rock bass. The agreement of the data for the fish from Allequash, Silver, and Trout Lakes was so close that a combination of all available collections from these three lakes was feasible. It is of some interest that the arrangement of the various populations with respect to relative heaviness follows the arrangement of the lakes as to the hardness of their waters. The heaviest rock bass were taken from Allequash, Silver, and Trout Lakes (16.8, 15.0, and 18.7 p.p.m., respectively, of bound CO₂), and the lightest fish came from Nebish Lake (4.0 p.p.m. of bound CO₂). Muskellunge Lake, with medium-hard water (10.0 p.p.m. of bound CO₂), contained rock bass that were intermediate in relative heaviness.

A summary of this paper may be found in the abstract.

LITERATURE CITED

HILE, RALPH

1941. Age and growth of the rock bass, *Ambloplites rupestris* (Rafinesque) in Nebish Lake, Wisconsin. Trans. Wis. Acad. Sci., Arts, and Let., Vol. 33, pp. 189-337.

WRIGHT, STILLMAN

1929. A preliminary report on the growth of the rock bass, *Ambloplites rupestris* (Rafinesque), in two lakes of northern Wisconsin. *Ibid.*, Vol. 24, pp. 581-595.
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AGE AND GROWTH OF THE YELLOW PERCH, *PERCA FLAVESCENS* (MITCHILL), IN THE WISCONSIN WATERS OF GREEN BAY AND NORTHERN LAKE MICHIGAN

RALPH HILE AND FRANK W. JOBES

INTRODUCTION

ALTHOUGH the yellow perch occurs in the shallower waters throughout the Great Lakes and is of considerable importance to both commercial fishermen and anglers in many localities, the chief centers of commercial production are Lake Erie, Saginaw Bay in Lake Huron, and Green Bay in Lake Michigan. Investigations of the age and growth of yellow perch in Great Lakes waters have been made of the Lake Erie perch by Jobes (MS) and of the Saginaw Bay perch by Hile and Jobes (1941).¹ The completion of the present study, the first on the growth of yellow perch in Lake Michigan, makes possible a comparison of the growth of the species in the three leading centers of production in the Great Lakes.

The study of the growth of the Green Bay yellow perch is of particular significance because of the contention of Wisconsin fishermen that this stock of perch grows at an exceptionally slow rate. The Green Bay fishermen believe also that the perch grows more slowly in the bay than in the open waters of Lake Michigan.

MATERIALS AND METHODS

The determination of age and the calculation of individual growth histories from the examination and measurement of scales were carried out for 752 yellow perch collected in Green Bay (see Fig. 1 for localities). An additional 90 fish, for which there were no sex

¹ Hile, Ralph, and Jobes, Frank W., "Age, Growth, and Production of the Yellow Perch, *Perca flavescens* (Mitchill), of Saginaw Bay," *Trans. Am. Fish. Soc.*, 70: 102-122, figs. 1-5. 1941.

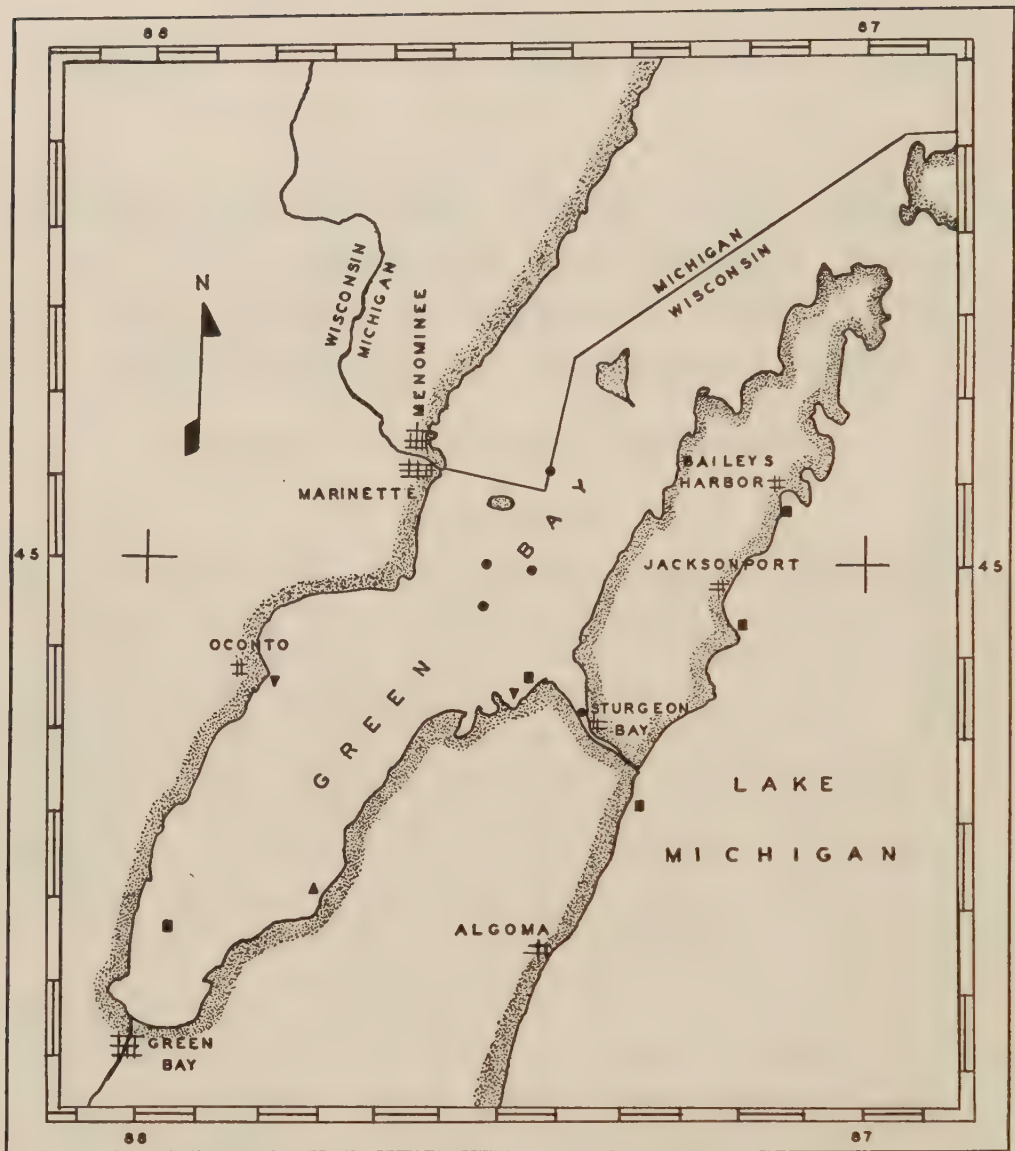


FIG. 1. Localities at which samples of eighteen or more yellow perch were taken in Green Bay and Lake Michigan: 1932, circles; 1934, upright triangles; 1937, squares; 1938, inverted triangles

data, were employed in the study of age composition (Table I), but their individual growth histories were not computed. All but the 1932 collections were taken in commercial gear. The details concerning the collections follow:

1932: 441 perch taken between April 27 and May 23, in experimental gill nets (mesh sizes: $2\frac{3}{8}$, $2\frac{1}{2}$, $2\frac{5}{8}$, and $2\frac{3}{4}$ inches, extension measure) fished from the Bureau of Fisheries vessel, *Fulmar*.

1934: 107 perch taken on March 24 in a 2-2 $\frac{1}{4}$ -inch-mesh pound net.

1937: 55 perch taken between November 26 and December 3 in a 2 $\frac{3}{8}$ -inch-mesh gill net and 3 (not included in Tables I and II, but included in body of Table IV) in a 2 $\frac{5}{8}$ -inch-mesh gill net; 74 fish taken on December 13 by a 2 $\frac{1}{4}$ -inch-mesh fyke net (includes one fish without sex data, not used in the growth study). Eighty-nine fish for which sex data were lacking, taken on November 12 in a 2 $\frac{3}{8}$ -inch-mesh gill net, were employed for the study of age composition but not of growth.

1938: 73 perch taken between March 22 and April 5 in pound nets and fyke nets whose mesh sizes ranged from 1 $\frac{3}{4}$ to 2 $\frac{5}{8}$ inches (more than half of the total from a 2-inch-mesh pound net).

In addition, ages were determined for five large fish selected for size.

The study of the relationship between the length and the weight of Green Bay yellow perch was based on 938 fish, including all specimens employed in the investigation of age and growth and also those perch whose ages could not be determined and several scattered selected samples (large fish selected for size, samples of illegal fish only, samples of legal fish only).

The relationship between total length and standard length was determined from measurements of 509 yellow perch from Green Bay and 360 from the Beaver Island region of northeastern Lake Michigan. No significant differences were found between the data from the two areas.

Collections of yellow perch totaling 276, taken in 2 $\frac{5}{8}$ -inch-mesh commercial gill nets between September 2 and October 13, 1937, were employed for the study of the age and growth of the perch in the Wisconsin waters of northern Lake Michigan (see Fig. 1 for localities). Ages of four large selected fish collected in 1937 and 1938 were also determined. The investigation of the length-weight relationship of perch in this area was based on 294 fish.

Scales for age determination were mounted in a glycerin-gelatine medium and examined and measured on a microprojection apparatus at the magnification $\times 40.7$. The calculation of growth was made by the method employed for the Saginaw Bay yellow perch (see note 1). In this procedure direct-proportion computations, based on the assumption that the body-scale ratio is constant, were employed for the determination of calculated lengths of 102 millimeters and greater. Calculated lengths less than 102 millimeters were "corrected" to compensate for the disproportionate growth of body and scale among smaller fish. It is realized that the correction of

the calculated lengths of the Green Bay and Lake Michigan yellow perch from a body-scale curve derived from Saginaw Bay materials may involve a certain degree of approximation. It is not believed, however, that the error was large.

Ages have been designated by roman numerals corresponding to the number of annuli on the scales, except for fish taken in the spring before the onset of growth. For these fish an annulus was "assumed" to be present at the edge of the scale, and the age assigned exceeded by one the number of visible annuli.

All materials and data obtained from Lake Michigan in 1937 and 1938 and from Green Bay in 1934, 1937, and 1938 were collected by investigators of the Wisconsin Conservation Department and made available to us through the courtesy of Dr. Edward Schneberger, chief of the Biology Division. The 1932 collections were made by Dr. Hilary J. Deason and other staff members aboard the Bureau of Fisheries vessel *Fulmar*. We wish also to thank Dr. John Van Oosten, in charge of Great Lakes Fishery Investigations of the U. S. Fish and Wildlife Service, for his numerous suggestions for the improvement of the original manuscript.

AGE COMPOSITION AND LENGTH DISTRIBUTION

The age composition of the samples of Green Bay yellow perch (Table I) varied widely, with the dominant age group as young as II and as old as V. The 1932 data suggest that mesh size of the gill nets employed had a significant effect on the age composition of the samples. The samples from the 2 $\frac{3}{8}$ -inch-mesh net were dominated by age group IV, whereas the samples from the larger mesh sizes all were dominated by age group V. The relative abundance of IV-group perch tended to decrease and the abundance of VI-group fish to increase with increase in the size of mesh.

Dominant age groups in samples from commercial gears (the 2 $\frac{3}{8}$ -inch-mesh experimental gill net fished in 1932 may be considered commercial gear) were age group II in the gill-net sample of 1937, age group III in the fyke-net collection of the same year and the pound-net collection of 1934, and age group IV in the collections of 1932 and 1938. It should be mentioned, however, that the 1937 collections were made in late fall and early winter, whereas the collections of the remaining years were taken in the spring. Consequently fish captured in 1937 had enjoyed one more season of growth

TABLE I

AGE COMPOSITION OF SAMPLES OF GREEN BAY YELLOW PERCH TAKEN IN DIFFERENT CALENDAR YEARS, IN DIFFERENT SEASONS, AND BY DIFFERENT FISHING GEAR (PERCENTAGES IN PARENTHESES)

Year and season	Kind of net, and mesh size in inches	Age group									Total
		I	II	III	IV	V	VI	VII	VIII	IX	
1932 (spring)	2 $\frac{3}{8}$ gill.....	...	2 (1.6)	2 (1.6)	68 (53.1)	41 (32.0)	14 (10.9)	1 (0.8)	...	...	128
	2 $\frac{1}{2}$ gill.....	...	...	2 (1.9)	32 (31.1)	43 (41.8)	26 (25.2)	...	...	...	103
	2 $\frac{5}{8}$ gill.....	...	...	1 (1.0)	27 (27.3)	50 (50.5)	21 (21.2)	...	...	...	99
	2 $\frac{3}{4}$ gill.....	...	1 (0.9)	1 (0.9)	21 (18.9)	53 (47.8)	31 (27.9)	4 (3.6)	...	...	111
1934 (spring)	2-2 $\frac{1}{4}$ pound.....	...	26 (24.3)	41 (38.3)	35 (32.7)	4 (3.8)	...	1 (0.9)	...	...	107
1937 (fall)....	2 $\frac{3}{8}$ gill.....	...	71 (49.3)	55 (38.2)	14 (9.7)	4 (2.8)	...	...	...	...	144
	2 $\frac{1}{4}$ fyke.....	2 (2.7)	21 (28.4)	44 (59.5)	7 (9.4)	...	...	...	...	...	74
1938 (spring)	1 $\frac{3}{4}$ -2 $\frac{5}{8}$ impounding.....	...	...	1 (1.4)	41 (56.2)	18 (24.6)	6 (8.2)	2 (2.7)	4 (5.5)	1 (1.4)	73
1932-38 (spring-fall)	All commercial gear *....	2 (0.4)	120 (22.8)	143 (27.1)	165 (31.4)	67 (12.7)	20 (3.8)	4 (0.8)	4 (0.8)	1 (0.2)	526

* Excludes catches of 2 $\frac{1}{2}$ -, 2 $\frac{5}{8}$ -, and 2 $\frac{3}{4}$ -inch-mesh gill nets in 1932

than had members of the same age groups in the collections of other years. A better idea of the age composition of the commercial catch may possibly be obtained from a compilation made in terms of completed growing seasons (Table II).

Yellow perch that had completed four seasons of growth made up nearly half (46.2 per cent) of the combined samples of the commercial catch. Next in abundance were perch that had completed three growing seasons (25.8 per cent) and five growing seasons (16.0 per cent). Other groups were represented only sparsely.

TABLE II

AGE OF GREEN BAY YELLOW PERCH TAKEN IN COMMERCIAL GEAR, EXPRESSED
IN TERMS OF THE NUMBER OF GROWING SEASONS COMPLETED

<i>Number of completed growing seasons</i>	<i>Number of fish</i>	<i>Percentage</i>
2	30	5.7
3	136	25.8
4	243	46.2
5	84	16.0
6	24	4.5
7	4	0.8
8	4	0.8
9	1	0.2

The age composition of the samples collected with 2 $\frac{5}{8}$ -inch-mesh gill nets in Lake Michigan in the fall of 1937 may be seen in Table III. Age group IV was dominant (42.7 per cent), and the combined age groups III and IV made up 78.2 per cent of the total. The only samples from Green Bay from 2 $\frac{5}{8}$ -inch-mesh gill nets (spring of 1932) were dominated by age group V. In terms of seasons of growth completed, however, these V-group fish correspond to the IV-group perch captured in Lake Michigan in the fall.

It is not believed that the data on the age composition of the samples of yellow perch from either Green Bay or Lake Michigan are suitable for an analysis of the relative abundance of the year classes represented. The chief defect of the data is the lack of adequate collections taken over a period of consecutive years by means of gear of the same type and mesh size. A further weakness of the data for the Green Bay perch lies in the fact that most of the collections were taken during the spawning run. In spawning-run samples the younger age groups that contain a high percentage of immature fish are not adequately represented.

TABLE III

AGE COMPOSITION OF THE SAMPLES OF YELLOW PERCH TAKEN IN THE FALL OF 1937 IN THE LAKE MICHIGAN WATERS OF DOOR COUNTY, WISCONSIN

<i>Age group</i>	<i>Number of fish</i>	<i>Percentage</i>
II	25	9.1
III	98	35.5
IV	118	42.7
V	27	9.8
VI	8	2.9

The length-frequency distributions of Green Bay yellow perch have been arranged in Table IV according to sex and the number of completed growing seasons (that is, with perch collected in the fall of 1937 combined with fish of the next higher age group of the spring collections of other years). As is commonly true of perch, the length distributions of fish of different ages exhibited considerable overlap, although this overlap doubtless was increased in the data for Green Bay perch by the combination of samples taken in different calendar years. All length intervals at which fish were abundant were represented by perch of three or four different ages. In fish of corresponding age the modal and average lengths of females consistently exceeded those of males.

Females attained the State of Wisconsin's legal size of $7\frac{1}{2}$ inches, total length (162 millimeters, standard length), earlier than males. (Although a 7-inch limit was in effect at the time of the collection of the materials employed in this study, the limit was raised to $7\frac{1}{2}$ inches on July 1, 1940, and is scheduled to be increased further to 8 inches, effective on July 1, 1943.) At the end of two growing seasons all males and females were below legal length. On the completion of three growing seasons, however, 96.0 per cent of the males though only 53.8 per cent of the females were undersized. Relatively few of the females (9.0 per cent) but a majority of the males (57.6 per cent) were below the length of $7\frac{1}{2}$ inches at the end of four growing seasons. Undersized perch of both sexes were scarce at the end of five and six growing seasons (no undersized females at the end of six seasons), and all fish were longer than $7\frac{1}{2}$ inches beyond the sixth year of life.

In the third and fourth columns from the right of Table IV may be seen the length-frequency distribution of all random samples of

TABLE IV
LENGTH-FREQUENCY DISTRIBUTION OF GREEN BAY YELLOW PERCH (COLLECTIONS OF ALL THE YEARS COMBINED)
ACCORDING TO SEX AND THE NUMBER OF COMPLETED GROWING SEASONS

At right, the length distribution of all samples from commercial gear in Green Bay and the length distribution of all samples from commercial gill nets in Lake Michigan

Standard length in millimeters	Age in completed growing seasons												Length distribution of commercial catch			
	2		3		4		5		6		7		8		9	
	M*	F*	M	F	M	F	M	F	M	F	M	F	M	F	F	
																Green Bay
	Num- ber †	Per- centage	Num- ber †	Per- centage	Num- ber †	Per- centage	Num- ber †	Per- centage	Num- ber †	Per- centage	Num- ber †	Per- centage	Num- ber †	Per- centage	Num- ber †	Per- centage
100-109	5	4	..	..	..	..	..	..	..	..	..	..	..	..	8	1.5
110-119	6	11	1	..	..	..	..	..	..	..	..	..	..	..	16	3.0
120-129	1	2	6	..	..	..	..	..	..	..	..	..	..	..	10	1.8
130-139	..	..	7	8	..	..	..	..	..	..	..	..	..	..	19	3.5
140-149	..	..	8	7	..	..	..	..	..	..	..	..	..	..	36	6.6
150-159	..	1	2	8	..	..	..	..	..	..	..	..	..	..	79	14.6
160-169	..	1	1	12	10	34	1	1	..	..	..	..	..	..	98	18.1
170-179	..	..	..	6	9	44	8	4	1	1	6	..	..	..	83	15.3
180-189	..	..	..	5	4	50	4	18	5	4	7	..	..	..	51	9.4
190-199	..	..	..	2	3	37	7	43	2	5	20	..	..	..	82	15.1
200-209	..	..	209	2	1	33	10	42	2	4	14	1	1	..	27	5.0
210-219	..	..	..	..	1	22	7	40	1	16	4	..	..	..	7	1.3
220-229	..	..	..	..	..	6	1	16	4	1	17	1	..	..	6	1.1
230-239	..	..	..	..	..	1	..	4	1	3	3	..	..	..	3	0.5
240-249	..	..	..	..	..	1	..	1	..	..	1	..	..	..	5	0.9
250-259	..	..	..	..	..	..	..	1	..	..	..	1	..	..	2	0.4
260-269	..	..	..	..	..	..	..	1	..	1	..	2	..	..	4	0.7
270-279	..	..	..	..	..	..	..	..	..	..	..	1	..	..	1	0.2
280-289	..	..	..	..	..	..	..	..	..	..	..	..	..	..	2	0.4
290-299	..	..	..	..	..	..	..	..	..	1	..	..	..	..	2	0.4
300-309	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	0.2
Number of fish	12	19	25	52	59	244	42	184	24	78	3	5	4	1	542	100.0
Average length	111	118	137	161	162	186	190	204	204	213	216	258	279	294	172	190
Percentage illegal §	100.0	100.0	96.0	53.8	57.6	9.0	7.1	1.1	4.2	0.0	0.0	0.0	0.0	0.0	30.8	1.4

* M = male; F = female

† Includes 16 fish whose ages were not determined

‡ Includes 14 fish whose ages were not determined

§ Less than 7½ inches, total length (162 millimeters, standard length)

Green Bay yellow perch taken in commercial gear. The percentage of undersized fish ($7\frac{1}{2}$ -inch size limit) in the samples of the commercial catch was 30.8. The percentages of illegal-sized perch at size limits of 7, 8, and $8\frac{1}{2}$ inches (an $8\frac{1}{2}$ -inch size limit is effective in the State of Michigan waters of the Great Lakes) were 21.5, 49.2, and 67.3, respectively.

The additional information that would be obtained from the presentation of length-frequency distributions of the age groups of Lake Michigan yellow perch is not sufficiently great to warrant the expansion of the tabular material. The length-frequency distribution of all Lake Michigan perch, however, is shown at the extreme right of Table IV. Of the 290 perch (including 14 whose ages were not determined) in samples of the commercial catch (taken by $2\frac{5}{8}$ -inch-mesh gill nets) only 1.4 per cent were below $7\frac{1}{2}$ inches in length. At size limits of 7, 8, and $8\frac{1}{2}$ inches the percentages of illegal-sized fish were 0.0, 9.0, and 34.8, respectively.

GROWTH IN LENGTH AND WEIGHT

The average lengths and weights of the age groups of Green Bay yellow perch at capture and the calculated growth histories of the age groups are given for the males in Table V and for the females in Table VI. The calculated lengths in these two tables exhibit numerous and at times large discrepancies. Some of these disagreements are doubtless the result of the small numbers of specimens in certain age groups. The remainder must be ascribed to other causes. The discrepancies are in general similar in the data for both sexes.

Lee's phenomenon of "apparent decrease in growth rate" with increase in the age of fish on which the calculations of growth are based occurred in the calculated lengths for the first three or four years of life. The second-year and third-year calculated lengths exhibited these systematic discrepancies most sharply. First-year lengths were affected less and fourth-year lengths only slightly. The calculated lengths in the later years of life gave no indication of the presence of Lee's phenomenon.

A detailed discussion of the probable causes of Lee's phenomenon in the calculated lengths of yellow perch need not be given since the problem has been treated thoroughly by Jobes (MS). Although no study was made of the body-scale relationship in the Green Bay

TABLE V
AVERAGE LENGTH AND WEIGHT AT CAPTURE OF MALE YELLOW PERCH FROM GREEN BAY AND THE AVERAGE
CALCULATED LENGTH ATTAINED BY THE AGE GROUPS AT THE END OF EACH YEAR OF LIFE

Age group	Year of capture	Number of fish	Weight in ounces	Total length in inches	Weight in grams	Standard length in millimeters	Calculated standard length in millimeters at end of year of life						
							1	2	3	4	5	6	7
VII	1932	3	6.2	10.0	176	216	57	91	130	151	175	200	216
VI	1932	20	5.9	9.6	167	209	57	93	121	151	180	209	...
	1938	2	3.5	8.0	99	174	62	93	125	144	162	174	...
V	1932	26	5.4	9.4	152	203	59	95	130	165	203	...	...
	1934	2	3.5	8.2	98	178	57	95	130	164	178	...	...
	1937	2	3.9	8.4	110	182	58	89	108	134	160	182*	...
	1938	7	3.4	7.9	97	172	65	99	124	147	172	...	...
IV	1932	7	4.3	8.7	121	189	58	96	140	189	...	...	...
	1934	15	2.1	6.9	59	147	59	94	123	147	...	...	...
	1937	7	3.3	7.7	94	166	62	95	122	148	166*	...	...
	1938	11	2.9	7.6	81	165	64	104	138	165	...	...	...
III	1934	21	1.5	6.3	43	134	66	104	134	163*	...	...	...
	1937	26	3.0	7.5	84	163	63	102	136	...	...	...	...
II	1934	12	0.8	5.2	22	111	67	111	154*	...	...	...	...
	1937	4	2.6	7.1	74	154	67	111	...	...	...	...	...
Grand average calculated length †							62	99	130	159	185	211	227
Annual increment of length							62	37	31	29	26	26	16
Number of fish							165	165	153	128	69	32	3

* Actual length at capture in November and December

† Beyond the fifth year of life the grand average calculated lengths were determined by the successive addition of the grand average annual increments of length to the grand average calculated length at the end of the fifth year

TABLE VI

AVERAGE LENGTH AND WEIGHT AT CAPTURE OF FEMALE YELLOW PERCH FROM GREEN BAY AND THE AVERAGE CALCULATED LENGTH ATTAINED BY THE AGE GROUPS AT THE END OF EACH YEAR OF LIFE

Age group	Year of capture	Number of fish	Weight in ounces	Total length in inches	Weight in grams	Standard length in millimeters	Calculated standard length in millimeters at end of year of life								
							1	2	3	4	5	6	7	8	9
IX	1938	1	24.0	13.5	680	294	55	79	121	165	189	212	236	260	294
	1938	4	18.8	12.8	533	279	60	90	120	172	216	243	264	279	...
VIII	1932	2	11.7	11.7	333	254	55	85	126	164	192	225	254	...	...
	1934	1	11.3	12.1	320	264	53	86	132	162	191	244	264	...	...
VII	1938	2	14.2	11.9	402	259	56	88	118	154	200	236	259	...	...
	1932	72	6.3	9.7	179	211	58	92	119	148	180	211	...	...	...
VI	1938	4	14.0	11.8	398	257	58	90	130	182	225	257	...	...	...
	1932	161	5.6	9.4	159	204	59	94	129	166	204	...	...	...	...
V	1934	2	3.2	8.1	92	175	59	93	116	154	175	...	...	...	...
	1937	1	3.6	8.0	102	173	50	78	112	134	154	173*	...	...	...
IV	1938	11	9.5	10.3	268	224	64	103	151	194	224	...	...	...	...
	1932	141	4.9	9.0	138	195	60	100	144	195	...	...	...	...	...
III	1934	20	2.7	7.5	76	162	62	99	134	162	...	...	...	...	...
	1937	10	4.1	8.3	116	180	62	100	129	156	180*	...	...	...	...
II	1938	30	3.5	7.9	100	172	64	104	144	172	...	...	...	...	...
	1932	6	2.9	7.3	81	158	62	108	157	...	...	...	...	...	...
I	1934	20	2.1	6.9	59	148	69	107	148	...	...	...	...	...	...
	1937	54	4.0	8.2	112	178	61	101	142	178*	...	...	...	...	...
I†	1938	1	2.9	7.6	82	165	76	115	165	...	...	...	...	...	...
	1932	3	0.8	5.2	22	112	68	112	...	...	...	...	...	...	...
I†	1934	14	0.8	5.3	23	114	67	114	...	...	...	...	...	...	...
	1937	25	3.4	7.9	95	171	68	116	171*	...	...	...	...	...	...
I†	1937	2	2.5	7.2	71	156	72	156*	...	...	...	...	...	...	...
	1937	2	2.5	7.2	71	156	72	156*	...	...	...	...	...	...	...
Grand average calculated length †							61	99	137	173	197	228	251	268	302
Annual increment of length							61	38	38	36	26	31	23	17	34
Number of fish							585	585	568	516	272	88	10	5	1

* Actual length at capture in November and December

† Beyond the fifth year of life the grand average calculated lengths were determined by the successive addition of the grand average annual increments of length to the grand average calculated length at the end of the fifth year

perch, it appears safe to state nevertheless that the discrepancies represent in the main real differences in the growth of the fish in the various age groups and not methodical errors traceable to the procedure followed in calculating growth. It can be stated also that the selective action of the fishing gear and selective destruction of the more rapidly growing individuals in the commercial fishery were doubtless among the most important factors contributing to the observed differences in the growth histories of the several age groups. Segregation according to size and maturity also may have played a significant rôle.

Rather large discrepancies occurred also between the corresponding calculated lengths of yellow perch that were members of the same age group but were collected in different calendar years. Perch of the 1932 collection, especially age groups IV and V, were large at capture and had large calculated lengths in the later years of life. This rapid growth of perch of the 1932 collection is believed to be in large measure the result of the use in that year of gill nets of mesh sizes greater than the $2\frac{3}{8}$ -inch mesh commonly employed by commercial fishermen in the Wisconsin waters of Green Bay. Evidence in support of the belief that nets with larger mesh sizes tend to select the larger fish may be found in Table VII, in which are shown the average lengths of some of the best-represented age groups as determined from the samples of gill nets of different mesh size.² Particular attention should be given to the data for the females, since males were represented so poorly that their average lengths were included only to show that the data for both sexes exhibited similar trends. With one exception the average length of the females of each age group increased with increase in the size of mesh. The differences between the average lengths of the age groups of females as determined from the sample of the $2\frac{3}{8}$ -inch-mesh net (approximately the equivalent of commercial gill nets) and as determined from the combined samples of all nets were: age group IV, 7 millimeters; age group V, 13 millimeters; and age group VI, 20 millimeters. The differences between the average lengths of female perch captured by $2\frac{3}{8}$ - and $2\frac{3}{4}$ -inch-mesh gill nets were: age group IV, 21 millimeters;

² Since it was believed that only those collections should be employed that had been taken in nets of different mesh size fished simultaneously, a collection from Sturgeon Bay, for the capture of which only the $2\frac{3}{4}$ -inch-mesh net was employed, was excluded in the preparation of Table VII.

TABLE VII

RELATIONSHIP BETWEEN THE MESH SIZE OF THE GILL NETS EMPLOYED IN TAKING THE SAMPLES AND THE AVERAGE STANDARD LENGTH IN MILLIMETERS OF THE REPRESENTATIVES OF CERTAIN AGE GROUPS IN THE 1932 COLLECTION OF YELLOW PERCH FROM GREEN BAY (NUMBER OF SPECIMENS IN PARENTHESES)

Mesh size (stretched measure in inches)	Length according to age group and sex					Average length of all perch taken in mesh *
	IV	V		VI		
	Female	Male	Female	Male	Female	
2 $\frac{3}{8}$	188 (65)	201 (5)	191 (36)	197 (5)	191 (9)	190 (133)
2 $\frac{1}{2}$	195 (31)	202 (7)	201 (36)	210 (7)	211 (19)	201 (106)
2 $\frac{5}{8}$	206 (27)	220 (1)	211 (49)	207 (2)	211 (19)	207 (106)
2 $\frac{3}{4}$	209 (10)	202 (2)	215 (27)	227 (1)	218 (22)	210 (113)
Average.....	195 (133)	203 (15)	204 (148)	206 (15)	211 (69)	201 (458)

* Includes other age groups and 17 fish whose ages were not determined

age group V, 24 millimeters; and age group VI, 27 millimeters. From these data it is apparent that the selective action of fishing gear may have a pronounced effect on the determination of the growth histories of samples of fish.

Fluctuations in growth rate from one year to another also may have contributed to the discrepancies between the calculated growth of yellow perch of the same age group collected in different years.

In spite of the rather large discrepancies in the calculated growth histories of Green Bay yellow perch of the same and different ages, it is believed that a general growth curve based on the combination of the collections from all years and localities and taken by various types of gear provides a reasonably reliable index of the rate of growth of the population. The grand average calculated lengths and increments of length at the bottoms of Tables V and VI (see also Table XI for a direct comparison of the growth of the sexes and Figure 3 for a graphical representation of the growth of Green Bay perch) reveal that perch of both sexes made by far the greatest growth in length

in the first year of life. The much smaller growth increments of the later years exhibited a distinct although at times an irregular downward trend. (The males showed this trend more clearly than did the females.) Beginning in the third year of life the calculated lengths of females exceeded those of males. This sex difference ranged from 7 millimeters at the end of the third year to a maximum of 24 millimeters at the end of the seventh. The legal length of $7\frac{1}{2}$ inches, total length (162 millimeters, standard length), was attained by the females in the latter part of the fourth year of life and by the males early in the fifth year of life. The ages at which lengths of 7, 8, and $8\frac{1}{2}$ inches were reached were: 7 inches, in the fourth year of life of both the males and the females; 8 inches, at the end of the fourth year of life of the females and about the middle of the fifth year of life of the males; $8\frac{1}{2}$ inches, about the middle of the fifth year of life of the females and at the end of the fifth year of life of the males.

The calculated weights of Green Bay yellow perch at the end of the different years of life (Table XII) correspond to the grand average calculated lengths, and were computed by means of the length-weight equation given on page 257. The calculated weights of males and females were the same at the end of the first and second years of life. In later years the females had an advantage that varied from 7 grams at the end of the third year of life to 83 grams at the end of the seventh. The averages for the sexes reveal that the Green Bay perch did not reach a weight of a quarter pound until the fifth year of life. The weight of a half pound was reached in the seventh year of life, and the females weighed more than a pound in the ninth year.

Since records of sex were not available for the collections of yellow perch from Lake Michigan, the discrepancies among the calculated lengths of the age groups (Table VIII) may depend in part on variations in the relative abundance of males and females at different ages. Other factors, mentioned previously, also doubtless contributed to the occurrence of Lee's phenomenon in the growth data for Lake Michigan perch. In spite of the lack of sex records the data of Table XI indicate conclusively that Green Bay fishermen are in error in their contention that perch grow more slowly in Green Bay than in Lake Michigan. The grand average calculated lengths of the Lake Michigan perch were well below the calculated lengths of female Green Bay perch in all years of life beyond the first and were

less than the calculated lengths of male Green Bay perch in every year of life but the sixth. The slow growth of perch in the samples from Lake Michigan cannot well be attributed to the selective action of gear since they were taken by gill nets of relatively large mesh ($2\frac{5}{8}$ inches, stretched measure).

The calculated growth in weight of Lake Michigan yellow perch (Table XII) was computed by means of the length-weight equation given on page 257. By reason of their more robust form their cal-

TABLE VIII

AVERAGE LENGTH AND WEIGHT AT CAPTURE OF YELLOW PERCH COLLECTED IN NORTHERN LAKE MICHIGAN IN SEPTEMBER, 1937, AND THE AVERAGE CALCULATED LENGTH ATTAINED BY THE AGE GROUPS AT THE END OF EACH YEAR OF LIFE (NO RECORDS OF SEX OBTAINED)

Age group	Number of fish	Weight in ounces	Total length in inches	Weight in grams	Standard length in millimeters	Calculated standard length in millimeters at end of year of life					
						1	2	3	4	5	6
VI	8	9.5	10.4	269	225	56	83	113	148	172	201
V	27	5.7	8.9	161	193	58	87	110	136	166	..
IV	118	5.6	8.9	158	193	61	92	118	159	..	..
III	98	5.1	8.6	144	187	61	99	145	..	..	..
II	25	4.2	8.2	120	177	64	116	..	..	..	..
Grand average calculated length *						61	96	128	154	183	212
Annual increment of length						61	35	32	26	29	29
Number of fish						276	276	251	153	35	8

* Beyond the fourth year of life the grand average calculated lengths were determined by the successive addition of the grand average annual increments of length to the grand average calculated length at the end of the fourth year

culated weights exceeded those of Green Bay perch in four of the six years of life for which comparisons were possible, and were equal to or only slightly less than the weights of Green Bay fish in the remaining two years of life.

The data for a number of selected large yellow perch from Green Bay and Lake Michigan provide some idea of the maximum size and age attained in those areas. The largest perch captured in Green Bay was a female with a total length of 14.3 inches (311 millimeters, standard length) and a weight of 26 ounces (737 grams).

This fish, which was taken one-half mile south of Marinette, was a member of age group VII. There is no record of the gear in which the fish was captured. The biological samples from Green Bay included a number of older fish but none so large. The largest perch from Lake Michigan were three females taken off Bailey's Harbor in 4½-inch-mesh gill nets on March 29, 1938. At capture each weighed 28 ounces (794 grams). The ages, total lengths in inches, and standard lengths in millimeters were as follows: age group VI, 13.8 inches, 300 millimeters; age group VII, 13.5 inches, 294 millimeters; age group IX, 14.3 inches, 311 millimeters.

TABLE IX

RATIO OF STANDARD LENGTH TO TOTAL LENGTH OF YELLOW PERCH FROM GREEN BAY AND THE BEAVER ISLAND REGION OF LAKE MICHIGAN

<i>Interval of standard length in millimeters</i>	<i>Ratio of standard length to total length</i>	<i>Number of fish</i>
149 and less	0.844	57
150-209	0.853	657
210 and more	0.858	155

In the preceding discussion corresponding total and standard lengths have been presented without a statement of the relationship between the two. Measurements of 869 yellow perch made possible the determination of the ratios of standard length to total length in fish of different sizes (Table IX).

LENGTH-WEIGHT RELATIONSHIP

Although the length-weight data of Green Bay yellow perch were tabulated originally according to sex and year of capture, the variation from year to year in the length distribution of the samples and the scarcity of males in some collections made a detailed analysis unfeasible. Data presented here will be limited to the general length-weight curve based on a combination of all available materials. It may be stated, however, that the Green Bay perch tended to be heaviest in relation to their length in 1937 and lightest in 1934. Females were heavier than males of corresponding length in 1932 and 1938, but were lighter in 1934. Sex differences were negligible in 1937. In the combined collections females averaged slightly heav-

ier than males (average coefficient of condition,³ K , of 1.85 as compared with a coefficient of 1.81 for males over the length intervals in which both sexes were represented).

The lack of sex records for all but a few selected individuals of the Lake Michigan collections prevented the determination of possible sex differences in the length-weight relationship of yellow perch from that area.

The comparison of weights and coefficients of condition of yellow perch from Green Bay and Lake Michigan by centimeter intervals of standard length (Table X) reveals that the Lake Michigan fish were much the heavier at the lengths represented by adequate numbers of individuals. This advantage is reflected also in the higher grand average K (2.18 in Lake Michigan; 1.87 in Green Bay). To some extent their greater weights may be held to represent real differences between the populations, although seasonal and annual fluctuations in the length-weight relationship may also have played a rôle.

The coefficients of condition of Green Bay yellow perch tended to increase with increase in length up to a length of 180 millimeters. This increase was followed by a decline over the interval, 180–219 millimeters, and an increase beyond the latter length. In the Lake Michigan perch the values of K tended to decline with increase in length among the smaller fish, but were extremely high at the greatest lengths.

The fitting of parabolas to the length-weight data⁴ yielded the following equations:

$$\text{Green Bay, } W = 0.9319 \times 10^{-5} L^{3.133}$$

$$\text{Lake Michigan, } W = 5.8405 \times 10^{-5} L^{2.811}$$

In both equations W = weight in grams and L = length in millimeters.

The solutions of these equations are represented graphically by the smooth curves of Figure 2. Comparisons with the empirical data reveal fairly good agreement within the intervals over which the equations were fitted. The weights of the longer fish from both

³ $K = \frac{W \times 10^5}{L^3}$, where W = weight in grams and L = length in millimeters.

⁴ The equations were fitted to the average lengths and weights by five-millimeter intervals of standard length.

TABLE X

LENGTH-WEIGHT RELATIONSHIP OF YELLOW PERCH FROM GREEN BAY
AND LAKE MICHIGAN

Interval of stand- ard length in milli- meters	Total length in inches equivalent to mid- point	Green Bay				Lake Michigan			
		Weight in grams	Weight in ounces	K	Num- ber of fish	Weight in grams	Weight in ounces	K	Num- ber of fish
100-109	4.9	19	0.7	1.62	10	...	...	...	...
110-119	5.3	25	0.9	1.63	22	...	...	...	...
120-129	5.8	34	1.2	1.74	39	...	...	...	...
130-139	6.3	45	1.6	1.81	33	...	...	...	...
140-149	6.7	58	2.0	1.88	44	...	...	...	...
150-159	7.1	71	2.5	1.92	83	96	3.4	2.48	3
160-169	7.6	84	3.0	1.91	100	104	3.7	2.30	14
170-179	8.0	105	3.7	1.95	91	121	4.3	2.23	70
180-189	8.5	120	4.2	1.89	106	138	4.9	2.15	84
190-199	9.0	136	4.8	1.84	110	157	5.5	2.11	50
200-209	9.4	157	5.5	1.84	117	181	6.4	2.14	44
210-219	9.8	178	6.3	1.83	95	214	7.5	2.17	11
220-229	10.3	207	7.3	1.85	43	261	9.2	2.26	9
230-239	10.8	240	8.5	1.90	20	...	...	...	...
240-249	11.2	288	10.2	2.04	10	295	10.4	2.01	1
250-259	11.7	370	13.1	2.34	2	391	13.8	2.28	3
260-269	12.1	406	14.3	2.18	4	...	...	...	...
270-279	12.6	436	15.4	2.13	2	...	...	...	...
280-289	13.1	624	22.0	2.67	2	473	16.7	2.02	1
290-299	13.5	652	23.0	2.57	2	709	25.0	2.79	2
300-309	14.0	598	21.1	2.14	2	794	28.0	2.94	1
310-319	14.4	737	26.0	2.45	1	794	28.0	2.64	1
Average or total	...	...	...	1.87	938	...	...	2.18	294

Green Bay and Lake Michigan were far greater than those computed from the length-weight equations.

At the attainment of Wisconsin's legal length ($7\frac{1}{2}$ inches, total length; 162 millimeters, standard length) Green Bay yellow perch had a weight of 2.8 ounces (78 grams) and Lake Michigan perch a weight of 3.4 ounces (95 grams). The weights at 7, 8, and $8\frac{1}{2}$ inches were 2.3, 3.4, and 4.1 ounces, respectively, in Green Bay and 2.8, 4.0, and 4.8 ounces in Lake Michigan. The advantages of the Lake Michigan perch at the three lengths were 0.5, 0.6, and 0.7 ounces.

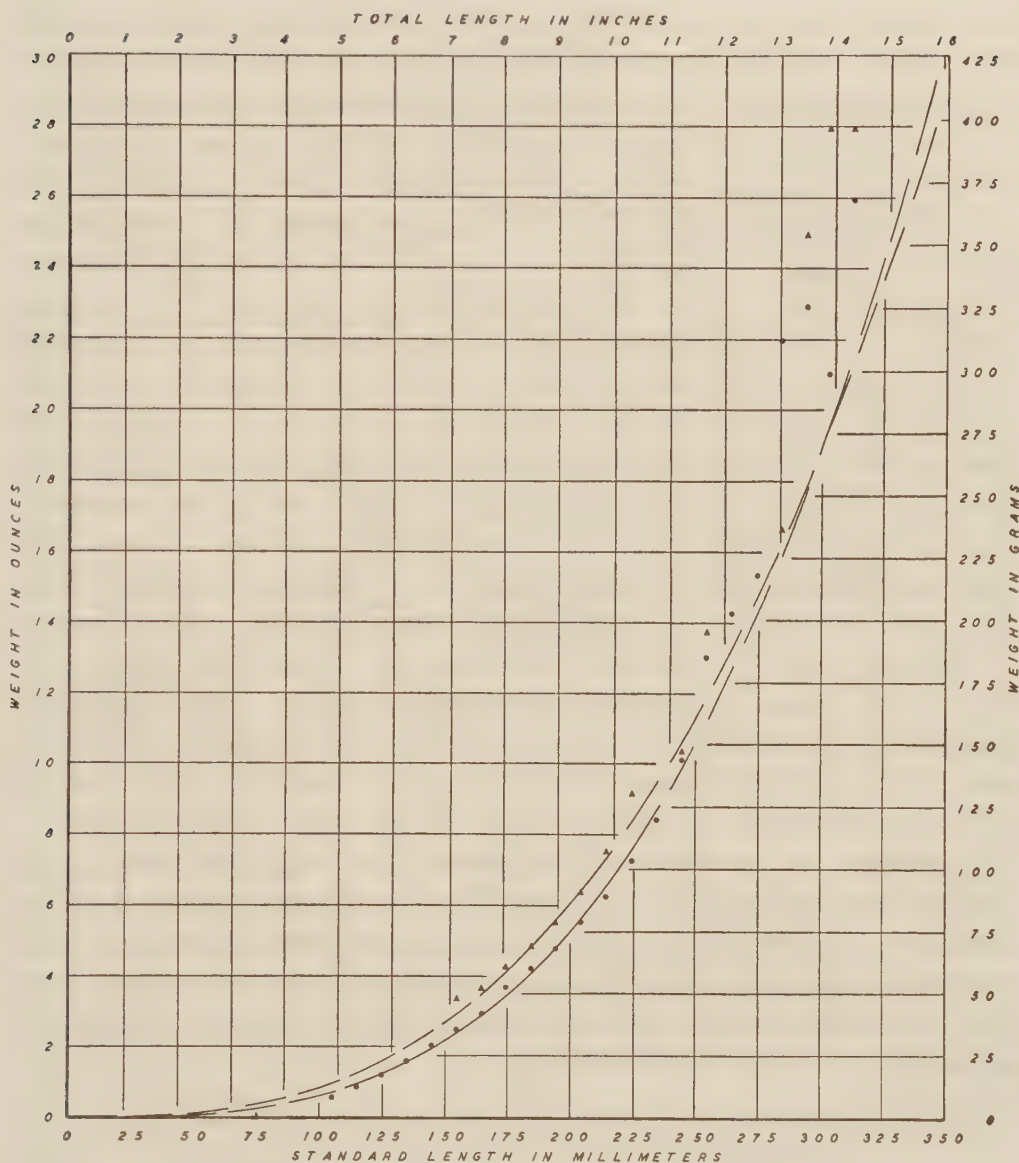


FIG. 2. Length-weight relationship of yellow perch (sexes combined) from Green Bay (circles) and northern Lake Michigan (triangles). The solid-line portions of the curves represent the range of lengths to which the equations were fitted

SIZE AT MATURITY AND SEX RATIO

Records of the state of maturity were obtained for the Green Bay yellow perch of the 1932 and 1934 collections. (The data on sexual maturity are based on 50 fish from bait nets of $1\frac{3}{8}$ -inch-mesh, 17 fish not aged in 1932, and 4 not aged in 1934, in addition to the

collections listed in Table I for 1932 and 1934.) Practically all the males (128 in a total of 133) and 85.0 per cent of the females (413 in a total of 486) were mature. Males were predominantly mature down to a total length of 5 inches. A majority of the females were immature at all lengths below 7 inches. More than half (58.8 per cent) were mature at 7 to $7\frac{1}{2}$ inches, and nearly all were mature above the length of $7\frac{1}{2}$ inches. It cannot be concluded, however, that most female Green Bay perch become mature at $7\frac{1}{2}$ inches, since the samples were taken during the spawning run in 1932 and shortly before the spawning run in 1934. Spawning-run samples tend to be made up almost entirely of mature fish. Unpublished data on the Lake Erie perch have demonstrated that the percentage of mature individuals at the lower lengths was much higher in spawning-run samples than in samples taken at other seasons. These Lake Erie data suggest that the length at which a majority of female Green Bay perch are mature is most probably greater than 7 to $7\frac{1}{2}$ inches.

The data on the relative abundance of the sexes in samples of Green Bay yellow perch were extremely variable. The number of females per 100 males ranged from 114 in 1934 to 688 in 1932 and was 356 for the collections of all the years combined. The change of the sex ratio with increase in age varied also. Males tended to become more abundant with increase in age in 1932 (a spring collection) and 1937 (a fall collection). No distinct trend was apparent in the data for the 1934 and 1938 collections (both taken in the spring). The data on the sex ratio of the Green Bay perch lend further support to the growing belief that the sexes may be segregated throughout much of the year.

COMPARISON OF THE GROWTH OF YELLOW PERCH IN GREEN BAY
AND NORTHERN LAKE MICHIGAN WITH GROWTH
IN LAKE ERIE AND SAGINAW BAY

Studies have been made of the age and growth of the Lake Erie yellow perch by Jobes (MS) and of the Saginaw Bay yellow perch by Hile and Jobes (see note 1). The data of Tables XI and XII and Figures 3 and 4 permit a comparison of the growth of perch in length and weight in four Great Lakes regions.

The calculated lengths of Lake Erie yellow perch were considerably greater than those of yellow perch from other areas of the Great Lakes during the first three years of life. The advantage of Lake

TABLE XI

COMPARISON OF GROWTH IN LENGTH OF YELLOW PERCH FROM FOUR
AREAS OF THE GREAT LAKES

Locality	Sex	Calculated standard length in millimeters at end of year of life								
		1	2	3	4	5	6	7	8	9
Lake Erie.....	Male	76	143	181	203	220	...	...	...	...
	Female	77	146	187	215	234	251	...	...	...
	Both *	76	144	184	209	227	...	...	...	...
Saginaw Bay.....	Male	65	114	166	204	232	259	275	...	...
	Female	65	116	174	211	236	270	293	...	...
	Both *	65	115	170	208	234	265	284	...	...
Green Bay.....	Male	62	99	130	159	185	211	227	...	...
	Female	61	99	137	173	197	228	251	268	302
	Both *	61	99	134	166	191	220	239	...	...
Northwestern Lake Michigan....	Both	61	96	128	154	183	212	...	...	...

* Unweighted mean

Erie perch over fish from Saginaw Bay was reduced from a maximum of 29 millimeters in the second year to 14 millimeters in the third and 1 millimeter in the fourth. At the end of the fifth year the Saginaw Bay perch were 7 millimeters longer than the Lake Erie fish. Comparisons of the calculated lengths of perch from Lake Erie and Green Bay reveal that the advantage of the Lake Erie perch increased from 15 millimeters at the end of the first year to a maximum of 50 millimeters at the end of the third and then declined to 36 millimeters at the end of the fifth year. The advantage of the Saginaw Bay perch over fish from Green Bay increased from 4 millimeters at the end of the first year to 45 millimeters at the end of the sixth and seventh years of life. The Green Bay fishermen seem to be correct in their belief that perch grow relatively slowly in the bay, although their belief that they grow more slowly in Green Bay than in Lake Michigan is in error. The calculated lengths of Lake Michigan perch were less than the lengths of Green Bay fish in all but the first year. The greatest difference (12 millimeters) occurred in the fourth year.

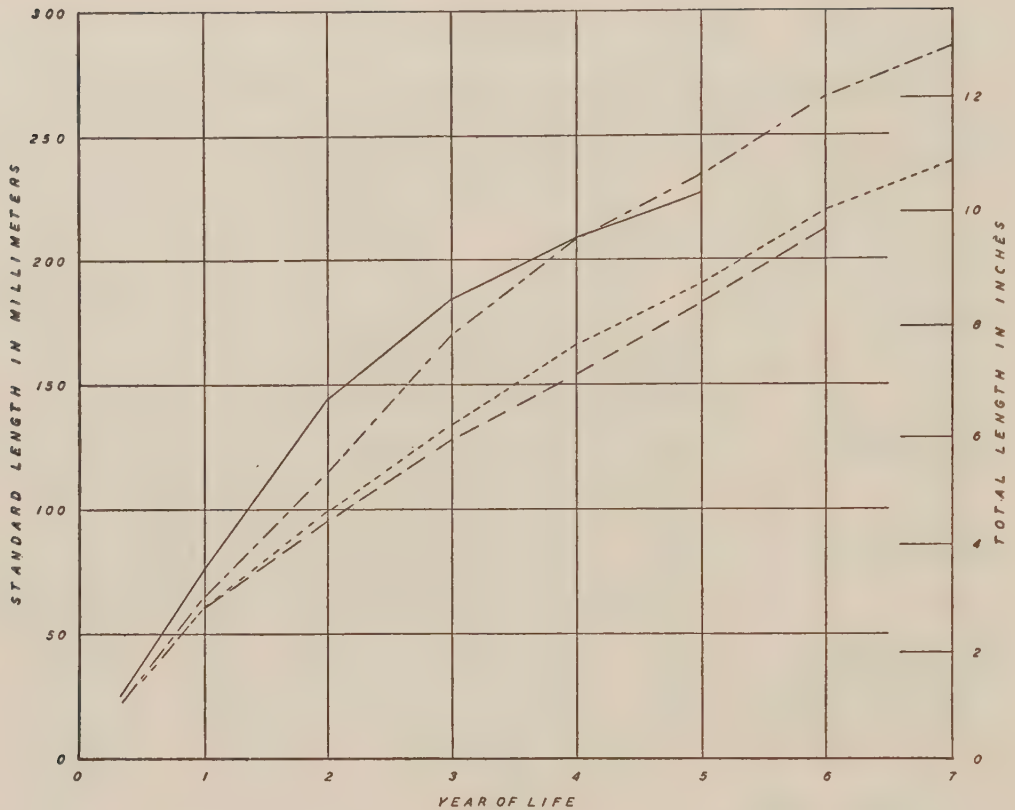


FIG. 3. Calculated growth in length of yellow perch (sexes combined): Lake Erie, —; Saginaw Bay, ----; Green Bay, ...; Lake Michigan, —·—·

The legal length of $8\frac{1}{2}$ inches, total length,⁵ was attained by the Lake Erie yellow perch in approximately three years and by the Saginaw Bay fish during the fourth growing season. The Wisconsin size limit of $7\frac{1}{2}$ inches, total length, was reached toward the latter part of the fourth growing season in Green Bay and in the early part of the fifth in Lake Michigan. In these two localities approximately five years were required for the attainment of the length of $8\frac{1}{2}$ inches, the size limit in Lake Erie and Saginaw Bay. On the other hand, Lake Erie perch reached a length of $7\frac{1}{2}$ inches, the size limit in the Wisconsin waters of Green Bay and Lake Michigan, at about the middle of the third growing season, and Saginaw Bay perch attained that length near the end of the third growing season.

⁵ Factors for conversions between standard and total length were slightly different in Lake Erie, Saginaw Bay, and Green Bay and Lake Michigan. The total lengths shown in Figure 3 corresponding to the various standard lengths are the averages of the values determined separately for fish of each of the three areas.

TABLE XII

COMPARISON OF THE GROWTH IN WEIGHT OF YELLOW PERCH FROM
FOUR AREAS OF THE GREAT LAKES

The calculated weights correspond to the calculated lengths of Table XI.

Locality	Sex	Calculated weight in grams at end of year of life								
		1	2	3	4	5	6	7	8	9
Lake Erie.....	Male	8	56	113	160	204	...	...	...	...
	Female	9	59	125	190	246	303	...	...	...
	Both *	8	57	119	175	225	...	...	...	...
Saginaw Bay.....	Male	4	25	82	156	233	328	395	...	...
	Female	4	27	95	173	245	373	482	...	...
	Both *	4	26	89	165	239	351	439	...	...
Green Bay.....	Male	4	17	39	73	118	178	224	...	...
	Female	4	17	46	96	144	227	307	377	548
	Both *	4	17	43	85	131	203	266	...	...
Northwestern Lake Michigan....	Both	6	22	49	83	134	203	...	...	...

* Unweighted mean

With respect to weight as well as length Lake Erie yellow perch were larger than yellow perch from Saginaw Bay during the first four years of life, but were smaller at the end of the fifth year. The greatest difference (31 grams) occurred at the end of the second year. The difference between the calculated weights of perch from Lake Erie and Green Bay increased progressively from 4 grams at the end of the first year of life to 94 grams at the end of the fifth year. Perch from Saginaw Bay and Green Bay had the same calculated weights at the end of the first year. In later years, however, the Saginaw Bay fish had an advantage ranging from 9 grams at the end of the second year of life to 173 grams at the end of the seventh. As mentioned previously (p. 255), the advantage of Green Bay perch over Lake Michigan perch with respect to growth in length did not include growth in weight. This difference with respect to growth in length and weight is to be explained by the fact that the yellow perch of the Lake Michigan population averaged somewhat heavier than the Green Bay fish of corresponding length.

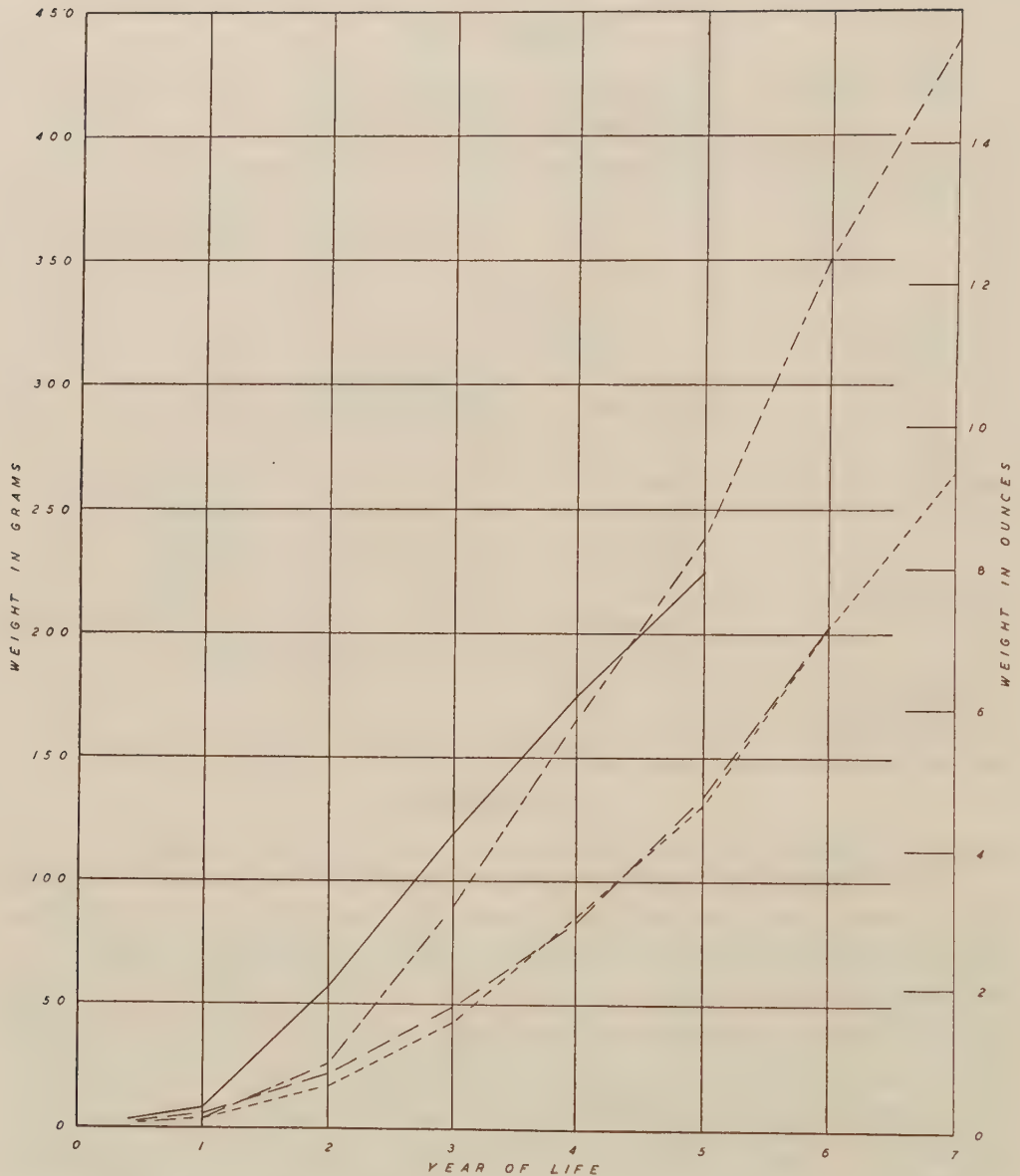


FIG. 4. Calculated growth in weight of yellow perch (sexes combined): Lake Erie, —; Saginaw Bay, ----; Green Bay, -.-.-; Lake Michigan, - - - -

SUMMARY

1. Ages of yellow perch were determined and individual growth histories were computed from the examination and measurement of the scales of 752 fish collected in 1932, 1934, 1937, and 1938 from the Wisconsin waters of Green Bay, and of 276 yellow perch taken from the Wisconsin waters of northern Lake Michigan in 1937. In

addition, ages were determined for 90 Green Bay perch for which sex records were lacking and for 9 large fish, selected for size, from both Green Bay and Lake Michigan. Sex records were lacking for all Lake Michigan perch except the large, selected individuals.

2. The numbers of fish employed for other phases of the investigation were: length-weight relationship, 938 from Green Bay and 294 from Lake Michigan; relationship between total length and standard length, 869 collected in Green Bay and northeastern Lake Michigan.

3. Samples of the commercial catch of Green Bay yellow perch were dominated by age groups II, III, and IV. Samples taken by experimental gill nets with mesh sizes larger than those employed in the commercial fishery were dominated by age group V. The collections from Lake Michigan were dominated by age group IV.

4. The length-frequency distributions of the age groups of Green Bay yellow perch exhibited extensive overlap. A majority of the females had reached the legal size of $7\frac{1}{2}$ inches, total length, at the end of four growing seasons, but a majority of the males did not attain this length till during the fifth year. In the combined samples from the catch of commercial gear 30.8 per cent of the perch were below the legal length of $7\frac{1}{2}$ inches. The samples from Lake Michigan contained only four (1.4 per cent) yellow perch less than $7\frac{1}{2}$ inches long.

5. The calculated growth histories of the age groups revealed some rather large discrepancies in the corresponding computed lengths of yellow perch of the same and different ages. The probable factors contributing to these discrepancies were mentioned briefly.

6. The general growth data showed that yellow perch of both sexes made by far the greatest growth in length during the first year of life. The growth increments of the later years exhibited a distinct although an irregular tendency to decrease. In the third and later years of life the grand average calculated lengths of females were larger than the corresponding lengths of males.

7. Green Bay fishermen are in error in their belief that yellow perch grow more rapidly in Lake Michigan than in the bay. The grand average calculated lengths of Lake Michigan perch (sexes combined) were less than the corresponding lengths of female perch from Green Bay in all but the first year of life and less than the corresponding lengths of male perch from Green Bay in all but the sixth year. Perch from Green Bay attained the legal length of $7\frac{1}{2}$

inches late in the fourth growing season; those from Lake Michigan, in the fifth season.

8. The calculated weights of Lake Michigan yellow perch tended to be slightly greater than those of Green Bay perch in corresponding years of life in spite of the slower growth in length of the Lake Michigan population.

9. The relationship between the length (L) of Green Bay yellow perch in millimeters and the weight (W) in grams was $W = 0.9319 \times 10^{-5} L^{3.133}$. The length-weight equation for Lake Michigan yellow perch was $W = 5.8405 \times 10^{-5} L^{2.811}$. In both populations the weights of the larger perch (beyond the length intervals over which the equations were fitted) tended to be higher than the weights computed from the equations. Lake Michigan perch almost always were heavier than Green Bay fish of corresponding length.

10. In samples taken immediately before and during the spawning run a majority of the male Green Bay yellow perch were mature down to a length of 5 inches and a majority of the females were mature at 7 to $7\frac{1}{2}$ inches. Spawning-run samples, however, tend to contain only mature fish; collections taken at other seasons probably would first show a majority of mature females at a length somewhat greater than 7 to $7\frac{1}{2}$ inches.

11. The sex ratio of yellow perch in the collections of the different years from Green Bay ranged from 114 females per 100 males in 1934 to 688 females per 100 males in 1932. The relative abundance of males tended to increase with increase in age in 1932 and 1937. In 1934 and 1938 no consistent changes were noted in the sex ratio with increase in age.

12. Comparisons of the calculated growth in length and weight of yellow perch from Lake Erie, Saginaw Bay, Green Bay, and northern Lake Michigan showed the Lake Erie perch to be the longest and heaviest during the first four years of life. At the end of the fifth year Saginaw Bay perch were longer and heavier than the Lake Erie fish. The growth of Green Bay perch was distinctly inferior to growth in Lake Erie and Saginaw Bay. Lake Michigan perch grew somewhat more slowly than the Green Bay perch in length but not in weight.

MATHEMATICAL RELATIONSHIP BETWEEN THE LENGTH AND THE AGE OF THE ROCK BASS, *AMBLOPLITES* *RUPESTRIS* (RAFINESQUE)

RALPH HILE

A NUMBER of species of fish, both marine and fresh-water, have been included among the animals employed for the investigation of the mathematical relationship between size and age. The equations derived have ranged in complexity from the relatively simple geometric-progression formulas developed by Ford (1933) for the marine herring and by Wagler for the northern pike (1936) and three species of coregonids (1937) to the rather complicated function applied by Pütter (1920) to the growth of Norwegian and Icelandic herrings. It does not come within the scope of this paper to undertake either a review of the various types of growth equations or a discussion of the logical and observational bases from which they were developed. Treatments of these subjects and numerous references to the literature may be found in publications by Pütter (1920), Ludwig (1929), von Bertalanffy (1934), Bückmann (1938), and others.

Directly pertinent to the subject of the present paper, however, is the growth formula derived by Weymouth and McMillin (1931) in connection with their investigation of the Pacific razor clam, *Siliqua patula*.¹ This equation, which was developed on the assumption, by no means new to biology, that the relative rate of growth decreases at a constant relative rate, took the form:

$$L = Be^{-ce^{-kt}},$$

where

$$L = \text{length,}$$

$$t = \text{time,}$$

and

$$B, c, \text{ and } k = \text{constants.}$$

¹ Although the Weymouth and McMillin equation was not fitted to data on the growth of fish, a point in common between the methods employed for the

The curve, which is of the Gompertz type,² fitted the empirical data satisfactorily except in old age, when the empirical values were higher than the calculated values.

A possible objection to the equation of Weymouth and McMillin lies in the fact that it was developed from assumptions concerning the instantaneous rate of growth, although the empirical data provided information only on the length of the clams at one-year intervals. Obviously the course of growth of cold-blooded animals (with a winter slackening or cessation of growth) does not proceed along the smooth and continuous curve of the Weymouth-McMillin formula. Instead, the growth must be recognized as a periodic function whose values are defined only at unit intervals of time. Rigorous procedure would require that the assumptions from which the growth formula is developed be concerned only with size at intervals of one year and with increments of growth for one-year periods.

It is of some interest to learn what type of equation results when the basic assumption (namely, that the relative rate of growth decreases at a constant relative rate) is the same as that employed by Weymouth and McMillin, but when this relative growth is expressed only in terms of growth over finite (one-year) intervals of time.

If the relative rate of growth, $\phi(t)$, decreases at a constant relative rate we have the relationship:

$$\frac{\phi(t+1)}{\phi(t)} = B,$$

where $B = \text{a constant } (0 < B < 1).$ (1)

It follows then that:

$$\phi(t) = CB^t. \quad (2)$$

$C = \text{a constant.}$

investigation of growth of certain mollusks and fish should be mentioned. Many species of both groups carry a history of past growth in the form of "winter rings" in the hard parts of the body (shells of mollusks; scales and bones of fish). A difference lies in the fact that the past growth of mollusks is measured directly on the shells, whereas the growth histories of fish are computed (by means of various formulas) from measurements of growth zones on scales or bones.

² See Winsor (1932) for a review of applications of the Gompertz curve to growth phenomena.

If size as a function of time is set as $f(t)$, we have by definition of the relative rate of growth:

$$\phi(t+1) = \frac{f(t+1) - f(t)}{f(t)} = CB^{t+1}. \quad (3)$$

From this relationship is obtained the final equation:

$$f(t) = K(CB + 1)(CB^2 + 1)(CB^3 + 1) \cdot \cdot \cdot (CB^t + 1). \quad (4)$$

$K = \text{a constant.}$

The final equation, which takes the form of a factorial, not only has an awkward appearance but presents the difficulty that the solution for $t = n$ requires the previous solution for all values of t less than n .

Considerable success was attained in fitting the equation to data on the growth of the 1923 year class of the rock bass, *Ambloplites rupestris*, of Nebish and Muskellunge lakes (Wisconsin). This year class was of such great abundance that large numbers could be taken at relatively advanced ages. Two circumstances contributed greatly to the reliability of the data as a true measure of the natural course of growth of rock bass in these lakes. The method of computing growth histories from scale measurements involved no large approximations, but was developed from a careful study of the actual relationship between body length and scale length. Furthermore, extensive data on the fluctuations (presumably from environmental causes) of growth rate in different calendar years made possible the "correction" of the growth curves for the year class to eliminate distortion of the data from that source.

The data of Tables I and II on the growth of the 1923 year class of the Nebish Lake rock bass are based on 117 males and 99 females captured in 1931 during the ninth year of life and on 41 males and 74 females taken in 1932 during the tenth year of life. In the tables are presented: the average calculated lengths (second column) and increments of length (third column) as actually computed from scale measurements; the quality of growth in different years expressed as percentages of average or "normal" growth (fourth column); the calculated increments of length (fifth column) and calculated lengths (sixth column) after "correction" to eliminate the effects of annual fluctuations in growth rate; the empirical values of the relative growth rate, $\phi(t)$ (seventh column); and the values of the ratio,

TABLE I

GROWTH OF MALE NEBISH LAKE ROCK BASS OF THE 1923 YEAR CLASS

Standard lengths and annual increments of length as computed originally from scale measurements and as corrected to eliminate the effects of fluctuations in the quality of growth (given in table as percentages of average or "normal" growth) in different calendar years. At the right of the table are the empirical values of the relative growth rate, $\phi(t)$, and of $\phi(t+1)/\phi(t)$.

Year of life	Calculated length in millimeters	Increment of length	Quality of growth in calendar year of increment	"Corrected" increment	"Corrected" calculated length	$\phi(t)$	$\frac{\phi(t+1)}{\phi(t)}$
1	37.1	37.1	112.8	32.9	32.9	...	...
2	63.2	26.1	90.9	28.7	61.6	0.8723	...
3	93.2	30.0	95.6	31.4	93.0	0.5097	0.5843
4	120.2	27.0	95.1	28.4	121.4	0.3054	0.5992
5	140.0	19.8	91.9	21.5	142.9	0.1771	0.5799
6	152.6	12.6	84.8	14.9	157.8	0.1043	0.5889
7	163.7	11.1	98.1	11.3	169.1	0.0716	0.6865
8	171.8	8.1	108.4	7.5	176.5	0.0444	0.6201
9	180.0	8.2	120.6	6.8	183.4	0.0385	0.8671

$\frac{\phi(t+1)}{\phi(t)}$ (eighth column). The method of computing growth histories from scale measurements and the procedure for determining annual deviations from average growth have been described by Hile (1941).

In the data for the male rock bass, only the first four values of $\frac{\phi(t+1)}{\phi(t)}$ tended to fluctuate about a constant level; beyond the sixth year of life, therefore, the growth of the males failed to conform to the style of growth assumed for the derivation of equation (4). For this reason, only the data on growth during the first six years were employed in fitting the equation to the observed calculated lengths. The curve for the females also was fitted to the data for the first six years, although the values of $\frac{\phi(t+1)}{\phi(t)}$ in Table II prove the selection of this period to be to a certain extent arbitrary.

Table III contains comparisons of the original growth data of the 1923 year class of the Nebish Lake rock bass with lengths computed from equation (4). At the bottom of the table may be found the values of the constants B , C , and K . The equation fitted the

TABLE II

GROWTH OF FEMALE NEBISH LAKE ROCK BASS OF THE 1923 YEAR CLASS

Standard lengths and annual increments of length as computed originally from scale measurements and as corrected to eliminate the effects of fluctuations in the quality of growth (given in table as percentages of average or "normal" growth) in different calendar years. At the right of the table are the empirical values of the relative growth rate, $\phi(t)$, and of $\phi(t+1)/\phi(t)$.

Year of life	Calculated length in millimeters	Increment of length	Quality of growth in calendar year of increment	"Corrected" increment	"Corrected" calculated length	$\phi(t)$	$\frac{\phi(t+1)}{\phi(t)}$
1	36.0	36.0	112.8	31.9	31.9	...	...
2	62.6	26.6	90.9	29.3	61.2	0.9185	...
3	90.5	27.9	95.6	29.2	90.4	0.4771	0.5194
4	113.8	23.3	95.1	24.5	114.9	0.2710	0.5680
5	130.8	17.0	91.9	18.5	133.4	0.1610	0.5941
6	141.6	10.8	84.8	12.7	146.1	0.0952	0.5913
7	149.9	8.3	98.1	8.5	154.6	0.0582	0.6113
8	156.5	6.6	108.4	6.1	160.7	0.0395	0.6787
9	164.5	8.0	120.6	6.6	167.3	0.0411	1.0405

TABLE III

COMPARISON OF THE GROWTH (STANDARD LENGTH IN MILLIMETERS) OF THE 1923 YEAR CLASS OF THE NEBISH LAKE ROCK BASS AS COMPUTED FROM SCALE MEASUREMENTS AND AS CALCULATED BY MEANS OF EQUATION (4)

The values of the constants of the equation for fish of each sex are given.

Year of life	Males			Females		
	Length from scale measurements	Length from equation	Difference	Length from scale measurements	Length from equation	Difference
1	32.9	32.9	0.0	31.9	32.0	0.1
2	61.6	61.6	0.0	61.2	60.1	- 1.1
3	93.0	93.2	0.2	90.4	90.1	- 0.3
4	121.4	121.3	- 0.1	114.9	115.7	0.8
5	142.9	142.9	0.0	133.4	134.3	0.9
6	157.8	157.8	0.0	146.1	146.6	0.5
7	169.1	167.5	- 1.6	154.6	154.2	- 0.4
8	176.5	173.5	- 3.0	160.7	158.8	- 1.9
9	183.4	177.2	- 6.2	167.3	161.4	- 5.9
Values of constants	<i>B</i> 0.5881 <i>C</i> 2.5238 <i>K</i> 13.2350			<i>B</i> 0.5682 <i>C</i> 2.7187 <i>K</i> 12.5854		

TABLE IV

GROWTH OF MALE MUSKELLUNGE LAKE ROCK BASS OF THE 1923 YEAR CLASS

Standard lengths and annual increments of length as computed originally from scale measurements and as corrected to eliminate the effects of fluctuations in the quality of growth (given in table as percentages of average or "normal" growth) in different calendar years. At the right of the table are the empirical values of the relative growth rate, $\phi(t)$, and of $\phi(t+1)/\phi(t)$.

Year of life	Calculated length in millimeters	Increment of length	Quality of growth in calendar year of increment	"Corrected" increment	"Corrected" calculated length	$\phi(t)$	$\frac{\phi(t+1)}{\phi(t)}$
1	33.8	33.8	104.9	32.2	32.2	...	...
2	50.8	17.0	102.0	16.7	48.9	0.5186	...
3	66.6	15.8	98.4	16.1	65.0	0.3292	0.6348
4	85.4	18.8	85.6	22.0	87.0	0.3385	1.0283
5	103.1	17.7	83.4	21.2	108.2	0.2437	0.7199
6	118.8	15.7	86.6	18.1	126.3	0.1673	0.6865
7	138.9	20.1	106.6	18.9	145.2	0.1496	0.8942
8	154.4	15.5	97.1	16.0	161.2	0.1102	0.7366
9	167.2	12.8	100.8	12.7	173.9	0.0788	0.7151

empirical data remarkably well over the first six years. The maximum deviations of the calculated lengths from the empirical values were 0.2 millimeter for the males and 1.1 millimeters for the females. The average deviations were 0.05 millimeter for the males and 0.62 millimeter for the females. The extrapolated portion of the curve, however, tended to fall below the empirical values. (The failure of growth formulas to describe growth late in life appears to be fairly common.)

The data of Tables IV, V, and VI on the 1923 year class of the Muskellunge Lake rock bass correspond exactly to the data given in Tables I, II, and III for the Nebish Lake rock bass. The numbers of fish on which the growth curves of the 1923 year class of the Muskellunge Lake rock bass were based were: 1930 — 18 males and 27 females in the eighth year of life; 1931 — 53 males and 68 females in the ninth year of life; and 1932 — 9 males and 10 females in the tenth year of life.

Although the values of $\frac{\phi(t+1)}{\phi(t)}$ varied more widely in the Muskellunge Lake rock bass than in the Nebish Lake rock bass, these variations were without detectable trend in the data for the Muskellunge

TABLE V

GROWTH OF FEMALE MUSKELLUNGE LAKE ROCK BASS OF THE 1923 YEAR CLASS

Standard lengths and annual increments of length as computed originally from scale measurements and as corrected to eliminate the effects of fluctuations in the quality of growth (given in table as percentages of average or "normal" growth) in different calendar years. At the right of the table are the empirical values of the relative growth rate, $\phi(t)$, and of $\phi(t+1)/\phi(t)$.

Year of life	Calculated length in millimeters	Increment of length	Quality of growth in calendar year of increment	"Corrected" increment	"Corrected" calculated length	$\phi(t)$	$\frac{\phi(t+1)}{\phi(t)}$
1	33.4	33.4	104.9	31.8	31.8	...	...
2	51.0	17.6	102.0	17.3	49.1	0.5440	...
3	66.3	15.3	98.4	15.5	64.6	0.3157	0.5803
4	83.3	17.0	85.6	19.9	84.5	0.3080	0.9756
5	98.7	15.4	83.4	18.5	103.0	0.2189	0.7107
6	112.1	13.4	86.6	15.5	118.5	0.1505	0.6875
7	131.0	18.9	106.6	17.7	136.2	0.1494	0.9927
8	144.4	13.4	97.1	13.8	150.0	0.1013	0.6780
9	153.8	9.4	100.8	9.3	159.3	0.0620	0.6120

TABLE VI

COMPARISON OF THE GROWTH (STANDARD LENGTH IN MILLIMETERS) OF THE MUSKELLUNGE LAKE ROCK BASS AS COMPUTED FROM SCALE MEASUREMENTS AND AS CALCULATED FROM EQUATION (4)

The values of the constants of the equation for fish of each sex are given.

Year of life	Males			Females		
	Length from scale measurements	Length from equation	Difference	Length from scale measurements	Length from equation	Difference
1	32.2	32.0	- 0.2	31.8	31.0	- 0.8
2	48.9	48.2	- 0.7	49.1	47.4	- 1.7
3	65.0	67.0	2.0	64.6	66.0	1.4
4	87.0	87.2	0.2	84.5	85.4	0.9
5	108.2	107.5	- 0.7	103.0	104.2	1.2
6	126.3	126.9	0.6	118.5	121.4	2.9
7	145.2	144.7	- 0.5	136.2	136.4	0.2
8	161.2	160.3	- 0.9	150.0	148.9	- 1.1
9	173.9	173.7	- 0.2	159.3	159.2	- 0.1
Values of constants	B 0.7736 C 0.8423 K 19.3985			B 0.7481 C 0.9399 K 18.2219		

Lake fish. In other words, the general style of growth of rock bass from Muskellunge Lake conformed approximately to that assumed originally throughout the nine years of life covered by the data, whereas in Nebish Lake the actual growth deviated notably from the theoretical beyond the sixth year of life.

The comparison of the theoretical lengths (equation based on data for all nine years of life) of Muskellunge Lake rock bass with the empirical calculated lengths reveals a reasonably good agreement. The average of the absolute values of the deviations was 0.67 millimeter for the males and 1.14 millimeters for the females. These average deviations were considerably larger than the corresponding deviations of 0.05 millimeter and 0.62 millimeter for the males and females of the Nebish Lake rock bass (first six years of life only).

The outstanding difference between the growth of the rock bass in Nebish Lake and that in Muskellunge Lake lies in the fact that in the former lake it deviated rather consistently from the theoretical curve beyond the sixth year, whereas in the latter the agreement between the lengths computed from the growth equation and the empirical lengths computed from scale measurements was fair throughout the nine years of life covered by the data. A possible explanation of this difference is suggested by the comparison of empirical and theoretical annual increments of length of rock bass of the two stocks (Table VII). In the Nebish Lake rock bass the empirical and theoretical increments of length agreed well during the first six years of life. It is true that in the data for the females differences as great as 1.2 and 1.1 millimeters occurred (second and fourth years of life, respectively). These maximum deviations were, however, of opposite signs and therefore most probably represent random errors. Beyond the sixth year of life the situation changed, for the empirical increments were consistently greater than the theoretical increments. The differences ranged from 1.5 to 3.1 millimeters in the males and from 0.9 to 4.0 millimeters in the females. In the Muskellunge Lake rock bass the differences between the empirical and the theoretical increments of length, although at times fairly large, apparently were distributed at random, that is, were not correlated with age.

The Nebish Lake data were characterized also by the extremely low values of the theoretical increments of length in the last three years of life (from 9.7 to 3.7 millimeters for the males and from 7.6

TABLE VII

COMPARISON OF INCREMENTS OF LENGTH (IN MILLIMETERS) OF NEBISH LAKE AND MUSKELLUNGE LAKE ROCK BASS AS COMPUTED FROM SCALE MEASUREMENTS AND AS COMPUTED FROM EQUATION (4)

Year of life	Nebish Lake				Muskellunge Lake			
	Males		Females		Males		Females	
	Com-puted from scale measurements	Com-puted from equation	Com-puted from scale measurements	Com-puted from equation	Com-puted from scale measurements	Com-puted from equation	Com-puted from scale measurements	Com-puted from equation
1	32.9	32.9	31.9	32.0	32.2	32.0	31.8	31.0
2	28.7	28.7	29.3	28.1	16.7	16.2	17.3	16.4
3	31.4	31.6	29.2	30.0	16.1	18.8	15.5	18.6
4	28.4	28.1	24.5	25.6	22.0	20.2	19.9	19.4
5	21.5	21.6	18.5	18.6	21.2	20.3	18.5	18.8
6	14.9	14.9	12.7	12.3	18.1	19.4	15.5	17.2
7	11.3	9.7	8.5	7.6	18.9	17.8	17.7	15.0
8	7.5	6.0	6.1	4.6	16.0	15.6	13.8	12.5
9	6.8	3.7	6.6	2.6	12.7	13.4	9.3	10.3

to 2.6 millimeters for the females). In Muskellunge Lake, however, the theoretical increments for these same years of life ranged from 17.8 to 13.4 millimeters for the males and from 15.0 to 10.3 millimeters for the females. It is suggested, therefore, that the failure of the growth of the Nebish Lake rock bass to follow the theoretical course during the later years of life may be ascribed to the exceptionally small theoretical increments of length during these years. With this explanation it is held that adherence beyond the sixth year of life to the style of growth that held during the first six years would involve a depression of the metabolic rate not compatible with the continued existence of the individual. In other words, the survival of the Nebish Lake rock bass to an advanced age may have been contingent upon a departure from the "normal" course of growth.

The extremely small theoretical length increments of the Nebish Lake rock bass in the later years of life may be traced to the rapid rate of decline of the relative rate of growth. The values of B (Table III) show that among the Nebish Lake males the ratio of the relative growth rate in a particular year of life to the relative growth

rate in the preceding year was on the average 0.5881 and that the corresponding ratio for the females averaged 0.5682 (both values based on growth in the first six years of life). The corresponding ratios for the Muskellunge Lake rock bass (based on growth throughout all nine years) were 0.7736 for the males and 0.7481 for the females (Table VI). The slower rate of decrease in the relative growth rate of the Muskellunge Lake fish accounted for the larger theoretical length increments in the later (sixth to ninth) years of life and may have made possible a survival to advanced ages without departure from the "normal" style of growth. It appears, then, that the rate of decrease of the relative growth rate may be of considerable biological significance.

I wish to thank Professor C. Eisenhart, of the University of Wisconsin, who read the manuscript critically.

SUMMARY

If it is assumed that the relative growth rate, as determined from annual increments of growth in length, decreases at a constant relative rate, the relationship between length (L) and age in years (t) may be expressed by the equation $L = K(CB + 1)(CB^2 + 1)(CB^3 + 1) \cdot \cdot \cdot (CB^t + 1)$, where K , C , and B are constants. This equation described accurately the growth of the 1923 year class of the rock bass from Nebish Lake (Wisconsin) during the first six years of life, but yielded values that were too low in the sixth to ninth years of life. The equation fitted reasonably well the data on growth of the 1923 year class of the rock bass from Muskellunge Lake (Wisconsin) over the nine years of life for which data were available. It was suggested that the theoretical increments of length (computed by means of the equation) of the Nebish Lake rock bass were so small that conformity in late years with the style of growth that prevailed during the first six years might well involve a depression of the metabolic rate not compatible with the continued existence of the individual. Thus in some populations survival to an advanced age may be contingent on a departure from the "normal" style of growth.

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LITERATURE CITED

- BERTALANFFY, LUDWIG VON. 1934. Untersuchungen über die Gesetzlichkeit des Wachstums. I. Teil: Allgemeine Grundlagen der Theorie; mathematische und physiologische Gesetzlichkeiten des Wachstums bei Wassertieren. Wilhelm Roux' Archiv für Entwicklungsmechanik der Organismen, 131: 613-652.
- BÜCKMANN, A. 1938. Über den Höchstertrag der Fischerei und die Gesetze organischen Wachstums. Berichte der deutschen wissenschaftlichen Kommission für Meeresforschung, N. F., 9:16-48.
- FORD, E. 1933. An Account of the Herring Investigations Conducted at Plymouth during the Years from 1924 to 1933. Journ. Marine Biol. Assn. United Kingdom, 19: 305-384.
- HILE, RALPH. 1941. Age and Growth of the Rock Bass, *Ambloplites rupestris* (Rafinesque), in Nebish Lake, Wisconsin. Trans. Wis. Acad. Sci., Arts, and Letters, 33: 189-337.
- LUDWIG, WILHELM. 1929. Vergleichende Untersuchung über Wachstumsgesetze. Biologisches Zentralblatt, 49: 735-758.
- PÜTTER, AUGUST. 1920. Studien über physiologische Ähnlichkeit. VI. Wachstumsähnlichkeiten. Pflügers Archiv für die gesamte Physiologie, 180: 298-340.
- WAGLER, E. 1936. Die Länge der Fische als Funktion des Alters. Allgemeine Fischerei-Zeitung, 1936 (4): 51-54.
- 1937. Die Coregonen in den Seen des Voralpengebietes. IX. Die Systematik der Voralpencoregonen. Internationale Revue der gesamten Hydrobiologie und Hydrographie, 35: 345-446.
- WEYMOUTH, F. W., AND McMILLIN, H. C. 1931. The Relative Growth and Mortality of the Pacific Razor Clam (*Siliqua patula*, Dixon), and Their Bearing on the Commercial Fishery. Bulletin, Bureau of Fisheries, 46: 543-567.
- WINSOR, CHARLES P. 1932. The Gompertz Curve as a Growth Curve. Proc. Nat. Acad. Sci., 18: 1-8.

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THE WHITEFISH FISHERY OF LAKES
HURON AND MICHIGAN WITH SPECIAL
REFERENCE TO THE
DEEP-TRAP-NET FISHERY

By John Van Oosten, Ralph Hile, and Frank W. Jobs

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ABSTRACT

This study of the whitefish fishery of Lakes Huron and Michigan includes: (1) a review of the available statistics of production, 1879-1942; (2) a detailed analysis of the annual fluctuations in the production and abundance of whitefish and in the intensity of the whitefish fishery in the State of Michigan waters of the lakes, 1929-1942, with special reference to the effects of fishing with deep trap nets; (3) an account of the bathymetric distribution and vertical movements of whitefish and certain other species; and (4) a report of field observations made in 1931 and 1932, as related particularly to the destruction of undersized whitefish by pound nets and deep trap nets. The main body of the manuscript and appendices A, B, and C, completed in March 1942, contain statistics through the year 1939. Since that time, records for the years 1940-1942 have become available. Because these additional data did not alter any of the conclusions of the manuscript but actually strengthened them, it was not deemed justifiable to expend the considerable amount of time and money that would be required to revise the study. The 1940-1942 records are therefore presented in appendix D.

From a relatively high production in the earlier years of the period, 1879 to 1942, the yield of whitefish declined to a lower level about which the catch fluctuated until the late 1920's and early 1930's when a general increase in production occurred. This recent increase was higher and the subsequent decline more severe in the Michigan waters of Lake Huron than in other areas.

THE WHITEFISH FISHERY OF LAKES HURON AND MICHIGAN WITH SPECIAL REFERENCE TO THE DEEP-TRAP-NET FISHERY¹



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GENERAL INTRODUCTION

The great economic value of the whitefish (*Coregonus clupeaformis*) and the widespread demand for it by the general public combine to make conservation of this species a matter of primary importance. Accordingly, conservation officials were gravely disturbed by the numerous reports and complaints of commercial fishermen in 1928, 1929, and 1930 concerning the operation of a new type of gear—the deep trap net—in the waters of Lake Huron off Alpena, Mich. These nets, the complainants contended, took whitefish literally by the tons, threatening the immediate extinction of the commercial stock. They held further that the deep trap net not only took legal-sized whitefish in unreasonable quantities but that it was also highly destructive to immature fish.

Gill-net fishermen stated that they were forced to suspend operations in areas in which deep trap nets were fished because of the thousands of rotting, undersized whitefish that drifted into their nets. These fish, they believed, had been destroyed in the deep-trap-net fishery. They charged specifically that young whitefish were killed by confinement in deep trap nets, by gilling in the trap-net meshes, by the rapid change of pressure when the nets were lifted, and by excessive and rough handling in the sorting of the catch. They charged further that deep-trap-net fishermen habitually dumped the dead, undersized whitefish overboard, and thus ruined the best whitefish grounds by polluting the bottom and driving away the fish.

Operators of both gill nets and pound nets objected to allegedly unfair tactics of deep-trap-net fishermen. Gill-netters stated that deep-trap-netters had usurped the traditional gill-net grounds and even had deliberately set deep trap nets across strings of gill nets. Pound-netters asserted that deep trap nets were set offshore in such positions as to block the passage of whitefish to the inshore pound-net grounds.

Both groups of fishermen complained that the high production by deep trap nets had glutted the market and depressed prices, making operations with other gears unprofitable.

The extent to which the many accusations leveled against deep trap nets and their operators were just could not be determined without extensive field observations. Preliminary inquiries, nevertheless, revealed that the deep trap net constituted an undeniably serious threat to the whitefish fishery. It was in recognition of this menace that the Michigan Department of Conservation and the United States Bureau of Fisheries (now the Fish and Wildlife Service) agreed to carry out cooperatively a program of field observation, in order first, to determine the effects of the deep trap net on the whitefish fishery, and second, to obtain information on which to base recommendations for sound regulation of the gear.

By 1931, the first year of the cooperative field investigations, the deep-trap-net fishery had expanded so rapidly that in a number of localities the net had become the dominant gear for the catching of whitefish. These nets were then being fished extensively in the State of Michigan waters of Lake Huron as far south as the "Middle Grounds" off the mouth of Saginaw Bay and had spread also into Lake Michigan where they were used in Green Bay and in northern Lake Michigan, out of Manistique and especially out of ports of the north channel area (region north of the Beaver Islands). In 1931 deep trap nets were fished also in the waters of Door County, Wisconsin. (For a condensed report of the brief survey of these waters in 1931 consult appendix C.)

The Michigan Department of Conservation's Patrol Boat No. 1 was placed at the service of the United States Bureau of Fisheries investigators from July 22 to 27, 1931, when a general survey of the deep-trap-net grounds of northern Lake Michigan and of Lake Huron was made. For the conduct of the later routine field observations, the Department of Conservation assigned one field assistant and paid the operating expenses of one automobile from August 1 to October 21, 1931, and during the month of May 1932. Beginning June 1, 1932, and extending into October, when the field work was discontinued, the Michigan Department of Conservation furnished three field assistants and paid the operating expenses of two automobiles. This increase of the staff made it possible to conduct the investigation simultaneously on both northern Lake Michigan and Lake Huron. The fishermen were practically all willing to cooperate by allowing

the investigators to go aboard their boats, by giving specific information requested, and by discussing frankly problems concerning the fishing industry on the Great Lakes.

The research staff of the U.S. Fisheries Vessel *Fulmar* obtained data in 1932 on some of the deep trap nets and pound nets fishing in Green Bay and around Gull Island in northern Lake Michigan.

The general procedure in the field investigation was to observe the lifting of the deep trap nets, to make counts of all fish in the net, and to take notes both from observation and interviews with the fishermen.

Certain data were, of necessity, obtained from the fishermen. They were: distance and direction from port or from some charted landmark; depth of water in which the net was set; size of mesh (as manufactured) in the lifting pot; depth of lead; and the dimensions of the net.

Other data were recorded as observed. These included: size of mesh (as found in use) in the lifting pot; preservative with which the twine was treated; numbers of legal- and illegal-sized fish, and of dead, bloated, and gilled fish of each species. Gilled whitefish were measured and weighed whenever possible. When it was impossible to measure or weigh the gilled fish, an estimate was made of the numbers that were of legal or illegal size. Lengths, weights, and scales were procured from samples of the catches of whitefish when possible. Few data could be obtained on the sex and maturity of the legal-sized whitefish because practically all were sold in the round.

The procedure for the study of pound nets was the same as that for the deep trap nets. As these two types of gear are of such similar construction, it has been possible in certain phases of the study to combine the data collected from both.

The data collected during the course of the 1931-1932 field investigations form the basis of parts III and IV of the present report.

Statistical investigations also have been made an integral part of the present study of the whitefish fishery of Lakes Huron and Michigan. In order to provide a better background for the understanding of conditions in the recent critical years, a compilation was made of all available statistics of production in the United States waters of the two lakes and of production in the Ontario waters of Lake Huron, beginning in 1879. These data are presented in part I.

Detailed statistical analyses have been made of local fluctuations in the production and abundance of whitefish and in the intensity of the whitefish fishery in the State of Michigan waters of Lakes Huron and Michigan over the period, 1929-1939 (part II). These analyses, which were based on commercial fishing reports supplied by the Michigan Department of Conservation, have contributed greatly to the understanding of the effects of extensive deep-trap-net operations on the general conditions of the fishery.

The deep trap net, with the effect of which on the course of the whitefish fishery this report is primarily concerned, was developed by the late John H. Howard at Cape Vincent, N.Y., and was first used by him in Lake Ontario in 1924. By experimentation Mr. Howard discovered that "the bigger the trap the bigger was the catch of fish taken."² Accordingly, he built larger trap nets, using his Lake Erie type of trap nets as a pattern, and increased their depth from about 12 feet to as much as 30 feet. This type of net soon was adopted by other fishermen in the vicinity of Cape Vincent, but apparently did not spread to other ports on Lake Ontario.

The deep trap net was introduced into Lake Huron July 12, 1928, when John H. Howard and his brother, D. C. Howard, set five nets in Thunder Bay off Alpena, Mich. Deep-trap-net operations were confined to the Alpena region in 1928 and 1929. In 1930, however, an expansion of the fishery got under way, that ultimately carried the deep trap net to all parts of the United States waters of Lake Huron and to most of the important whitefish grounds of Lakes Michigan and Superior.

In all three of these lakes the deep-trap-net fishery was confined to, or underwent its principal development in, the State of Michigan. Since deep trap nets were never permitted in the Province of Ontario or introduced into the Minnesota and Wisconsin

² We are indebted to the late John H. Howard and to J. P. Snyder, former Superintendent of the Federal Fish Hatchery, Cape Vincent, N. Y., for information on the deep trap net in Lake Ontario.

waters of Lake Superior, operations with the gear in Lakes Huron and Superior were limited to Michigan waters. Deep trap nets were fished in Lake Superior as far west as Ontonagon but were most abundant in Whitefish Bay at the eastern end of the lake. The use of deep trap nets became illegal in the Michigan waters of Lake Superior, July 1, 1936. The most extensive deep-trap-net fisheries of Lake Michigan were developed in the State of Michigan waters of Green Bay and of the northeastern section of the lake. Relatively limited operations were carried on also in Michigan waters off Grand Haven (chiefly in 1934), in the Wisconsin waters off Door County (1931-1935), and in Indiana (June 1935-July 1, 1936). The use of deep trap nets became illegal in the Michigan and Wisconsin waters of Lake Michigan after the 1935 season and in Indiana, effective July 1, 1936. This type of gear was never used in Illinois. The deep trap net may now be legally operated in the Great Lakes only in Lake Huron (Michigan waters) and Lake Ontario (New York waters).

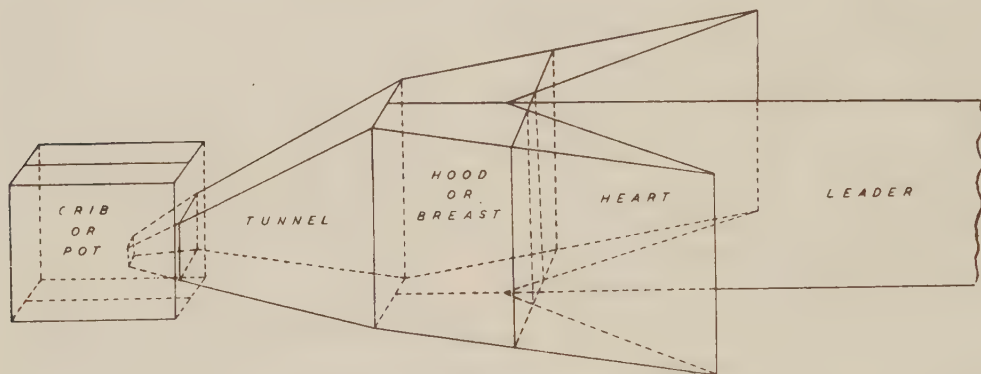


FIGURE 1.—The deep trap net.

The deep trap net (fig. 1) consists of the leader, hearts, hood or breast, tunnel, and lifting pot or crib.

The lifting pot or crib of the deep trap net is covered with webbing, whereas that of the pound net is open at the top. Deep trap nets are held in position by means of anchors and buoys while pound nets are generally held in position by stakes driven in the lake bottom. Aside from these two differences, deep trap nets and pound nets are of similar construction. In fact, during the earlier years of the deep-trap-net fishery the gear frequently was termed a "submarine pound net."

In the nets observed,³ the anchors were 2-point hook anchors weighing about 35 pounds each except the "king" anchor which weighed about 60 pounds. The smaller anchors (usually numbering 12 to 16) were attached to lines that varied from 400 to 600 feet in length; the "king" line attached to the back of the crib was about 1,800 feet long. The leader was from 40 to 80 rods long, from 20 to 47½ feet deep, and had meshes of 7 to 9 inches. (All mesh sizes in this description are extension measure as manufactured.)

The hearts had the same depth as the leader. The size of mesh in the hearts was reported to have ranged from 5 to 7 inches. The hearts were about 45 feet long with a spread of approximately 100 feet between the tips. In some nets the outside walls of the hearts were extended forward about 24 feet as single thicknesses of netting known as wings. The hood or breast, which connects the hearts and the tunnel, varied from 24 to 27 feet in length.

The tunnel, the length of which varied from about 45 to 75 feet, tapered from a depth equal to that of the hearts to form a 3-foot square opening inside the pot. Meshes in the part of the tunnel outside the pot varied from 5 to 7 inches, but meshes as small as 2 inches were reported for the tunnel inside the pot. Variations reported in the length

³ The dimensions given in this description were obtained from the fishermen and based on those nets observed in the field and possibly may not cover the full range of variation in the size of deep trap nets. It was, for example, reported to us that one fisherman operated a net that was 75 feet deep.

and depth of the lifting pot were: depth—18 to 47½ feet; length—30 to 40 feet. The lifting pot usually tapered from front to rear so that the width in a single net varied from about 24 to 20 feet. Mesh sizes in the pots ranged from 3½ to 5 inches as manufactured⁴ except that the front side of the net (the side through which the tunnel enters) contained meshes measuring not more than 3½ inches. In some nets this small mesh was extended along the sides and bottom of the net, but for a distance of not more than one third the length of the pot.

The lifting methods employed varied considerably, the most general method being that in which the net was brought to the surface by means of a lifting line attached to the "king" anchor line 75 to 150 feet from the back of the pot. When the net was brought to the surface, the boat was pulled under the anchor line and worked forward until it was under the pot of the net. The fish were shoaled on the front or tunnel side of the net and removed through laced openings. After the fish were removed, the boat was worked back to the point where the lifting line was attached, the lines were allowed to slip into the water, and the net was permitted to settle to the bottom. The average time required to lift a deep trap net was approximately one hour. Numerous mechanical devices have been developed to reduce the amount of labor involved and several types of power lifting machines are now in use. Some fishermen released the tension on the back anchor line and handled the net alongside the boat in a way similar to that employed for lifting pound nets.

⁴ The present minimum size of mesh permitted in the pots of deep trap nets operated in the Michigan waters of Lake Huron is 4½ inches as found in use; provision is made for a section of netting the meshes of which may not be more than 3½ inches on which the fish may be shoaled.

PART I

PRODUCTION OF WHITEFISH IN LAKES HURON AND MICHIGAN, 1879-1939

LAKE HURON

Because of defects in the data on the catch of whitefish in the United States (State of Michigan) waters of Lake Huron in certain of the earlier years, the graphical representation (fig. 2) of the production history of the lake (table 1) begins with the year

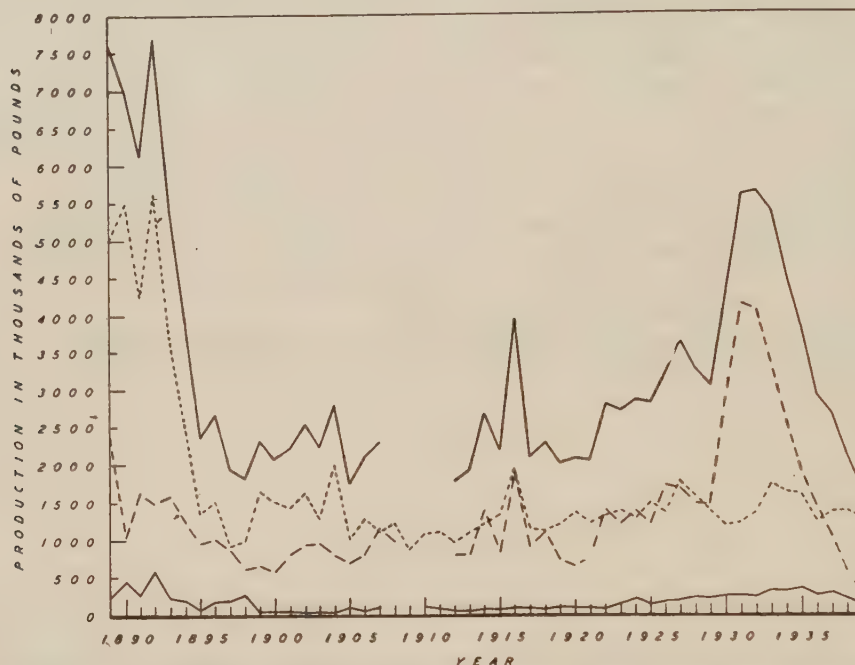


FIGURE 2.—Commercial production of whitefish in Lake Huron, 1889-1939. Lower solid line, Ontario waters of Huron proper; short dashes, North Channel and Georgian Bay; long dashes, State of Michigan waters; upper solid line, entire lake.

1889.⁵ It is true that data are available for Ontario waters of Lake Huron for years prior to 1889. However, it is with the course of production in the State of Michigan waters that the present study is most concerned.

Despite the known inclusion of the catch of Menominee whitefish or pilots⁶ in the data for 1879, 1885, and 1890, the recorded production of whitefish in the State of Michigan waters of Lake Huron exceeded 2 million pounds in only 2 of the 4 earliest years for which records are available (1879 and 1889) and was less than 1½ million pounds in 1885 and 1890 (only slightly above a million in the latter year).

The production of whitefish in the State of Michigan waters of Lake Huron was well over 2 million pounds in 1889, the first year for which acceptable data are available. In 1891, the second year for which presumably usable statistics are available, this yield was somewhat above 1½ million pounds. The next several years saw an irregular but distinct downward trend. The average production for the years, 1889

⁵ See appendix A for a listing of the sources of the statistical data of table 1 and statements concerning their limitations in certain years. Also see appendix D for the 1940-1942 records.

⁶ Although there can be no certainty concerning the production of Menominee whitefish in the early years of the fishery, it is not believed that catches of that species made up a great part of the reported production of whitefish in years earlier than 1891. Consequently, the catch for 1890 was graphed in figure 2 although the yield for that year was excluded from the computation of averages. The catch of Menominee whitefish in the State of Michigan waters of Lake Huron exceeded 100,000 pounds only 6 times in the 32 years for which data are available within the period, 1893-1939, and frequently was less than 50,000 pounds.

and 1891-1896 (1896 was the last of the earlier years in which the catch exceeded a million pounds), was 1,464,000 pounds. (In the discussion of this section, yields will be given to the nearest thousand pounds.) The period, 1897-1921, was one of rather consistently low output, the catch of whitefish exceeding a million pounds in only 4 isolated years of the 22 for which there are records. The average annual yield for this period was 885,000 pounds.

TABLE 1.—*Production of whitefish in pounds in Lakes Michigan and Huron, 1879-1939*

[See appendix A for list of sources of the data]

Year	Lake Michigan			Lake Huron			
	Wisconsin	Michigan	Entire lake ¹	Michigan	Ontario Huron proper	Ontario Georgian Bay	Entire lake
1879			\$12,030,400	\$2,700,778	726,600	864,800	\$4,292,178
1880					762,800	1,540,400	
1881					907,000	2,178,523	
1882					836,500	1,838,485	
1883					620,000	1,668,392	
1884					701,750	1,640,946	
1885	\$1,733,675	\$6,672,225	\$8,652,986	\$1,425,380	757,100	1,421,160	\$3,603,640
1886					557,000	1,823,849	
1887					325,600	2,664,406	
1888					236,550	4,946,788	
1889	481,955	5,004,641	5,523,971	2,391,503	210,219	5,003,259	7,604,981
1890	187,442	\$4,281,921	4,056,841	\$1,033,158	442,020	5,498,800	\$6,973,978
1891		2,404,571		1,624,860	267,900	4,236,880	6,129,640
1892	334,080	2,522,402	2,856,482	1,486,183	578,050	5,630,106	7,694,339
1893	470,325	1,975,800	2,446,125	1,577,600	226,000	5,645,800	5,449,400
1894	417,100	1,295,805	1,712,905	1,218,250	187,600	2,509,436	3,915,286
1895	520,325	1,022,740	1,543,065	945,867	58,230	1,355,275	2,359,372
1896	553,000	1,447,300	2,000,300	1,005,735	188,520	1,498,180	2,672,435
1897	886,358	2,418,953	3,345,071	865,960	172,570	910,466	1,948,996
1898		2,320,100		592,750	249,340	968,590	1,810,680
1899	125,355	1,633,880	1,769,793	645,580	28,074	1,651,086	2,324,740
1900		1,625,600		555,420	26,154	1,503,101	2,084,675
1901		2,079,550		788,245	23,606	1,413,239	2,225,090
1902		2,723,350		913,530	17,018	1,621,540	2,552,088
1903	116,764	2,284,600	2,404,269	937,460	19,630	1,279,060	2,236,150
1904		2,501,700		787,360	16,500	2,002,870	2,806,730
1905		2,570,100		674,860	78,980	994,050	1,747,890
1906		2,820,700		791,720	45,300	1,273,850	2,110,870
1907		3,273,800		1,132,972	82,020	1,095,220	2,310,212
1908	116,900	3,106,095	3,287,995	973,905	\$875,292	1,211,251	3,060,448
1909	133,253				4354,405	861,721	
1910	77,561				92,332	1,072,665	
1911	124,519	1,305,447	1,429,966		70,352	1,104,336	
1912	180,283	1,157,510	1,337,793	781,739	38,738	965,821	1,776,298
1913	117,925	1,202,299	1,320,224	787,101	39,017	1,105,683	1,931,801
1914	40,665	1,331,364	1,372,029	1,393,139	69,608	1,211,499	2,674,246
1915	120,916	1,358,838	1,479,754	812,286	56,859	1,335,484	2,204,629
1916	108,221	1,521,107	1,629,328	1,919,369	77,160	1,944,109	3,940,638
1917	126,933	2,458,084	2,622,767	888,977	76,535	1,144,620	2,110,132
1918	254,079	2,062,334	2,346,413	1,101,948	65,668	1,123,608	2,291,224
1919	202,119	1,286,601	1,488,720	727,194	97,419	1,200,842	2,025,455
1920	131,433	805,558	936,991	646,696	83,094	1,354,506	2,084,296
1921	362,415	958,709	1,321,124	757,616	78,493	1,222,676	2,056,785
1922	163,201	1,151,250	1,335,251	1,401,347	68,111	1,323,390	2,792,848
1923	442,923	1,061,701	1,504,624	1,198,971	128,909	1,390,021	2,717,901
1924	247,104	1,149,683	1,396,787	1,381,694	193,122	1,282,569	2,857,385
1925	242,379	1,405,028	1,652,000	1,203,149	121,524	1,495,881	2,820,554
1926	325,420	1,537,554	1,875,068	1,722,757	155,351	1,365,055	3,243,163
1927	314,232	2,254,623	2,591,291	1,676,875	191,494	1,773,983	3,642,093
1928	554,067	2,956,146	3,525,667	1,468,801	224,262	1,568,267	3,261,330
1929	644,489	4,287,869	4,968,733	1,456,368	204,761	1,385,316	3,046,445
1930	559,028	4,812,825	5,382,548	2,879,440	246,551	1,186,319	4,312,310
1931	841,639	3,823,983	4,675,277	4,139,772	245,157	1,214,918	5,599,847
1932	491,606	3,332,284	3,836,340	4,050,334	219,227	1,362,809	5,632,370
1933	332,000	2,235,840	2,574,440	3,333,901	309,519	1,733,056	5,376,476
1934	246,000	1,932,178	2,182,778	2,568,233	308,939	1,635,832	4,513,004
1935	263,900	1,431,724	1,697,124	1,894,807	340,327	1,596,312	3,831,446
1936	142,600	876,411	1,025,511	1,442,169	235,304	1,244,030	2,921,503
1937	122,300	946,867	1,072,967	1,018,681	286,981	1,377,130	2,682,792
1938	141,800	1,117,079	1,258,879	557,969	205,230	1,381,841	2,146,040
1939	110,700	839,856	950,556	255,183	115,061	1,275,255	1,645,499

¹ See appendix A for list of years in which the Lake Michigan total includes the catches in the waters of Illinois and Indiana.² Includes blackfins, longjaws, and pilots (Menominee whitefish); the total for the lake in 1890 does not include the catch of these three species.³ Includes pilots; the totals for the lake include only the pilots from the State of Michigan waters.⁴ Accuracy considered questionable; see p. 381.

The production of whitefish in the State of Michigan waters of Lake Huron rose to a higher level in 1922 and was consistently between 1 and 2 million pounds through the period, 1922-1929. The average catch for the 8 years was 1,439,000 pounds, practically the same as that for 1889 and 1891-1896.

In 1930, the whitefish fishery entered a period of chaotic change. The production of 2,879,000 pounds in this year was nearly double that of 1929 and was greater than that of any previous year. A further increase carried the yield of whitefish to an all-time high of 4,140,000 pounds in 1931. The 1932 output (4,050,000 pounds) was only a little below the record catch. In the years following 1932, whitefish production declined rapidly. This decline culminated in a 1939 yield of only 255,000 pounds, less than half the lowest production recorded for any previous year (555,000 in 1900). Detailed treatment of the violent fluctuations in the catch of whitefish in the State of Michigan waters of Lake Huron over the period, 1930-1939, is given on pp. 317-333. There evidence is presented that the high production in the earlier years of the period was made possible in large measure by the use of deep trap nets, and that this excessive yield in turn brought about a depletion of the stock that was responsible for the great severity of the subsequent decline.

The history of production of whitefish in the State of Michigan waters of Lake Huron may be summarized as follows. An early period of relatively high but decreasing yield (1889-1896) was followed by a long period (1897-1921) over which the catch was fairly stable at a rather low level. Production was stable in the years, 1922-1929, also, but the level of the take was considerably higher than that of the period, 1897-1921. The most recent period of the fishery (1930-1939) was one of violent fluctuations. Production rose suddenly to an all-time peak in 1931 of more than 4 million pounds only to decline to an all-time low in 1939 of $\frac{1}{4}$ million pounds. The normal annual take may be estimated as 1,114,000 pounds, the average catch per year for the period, 1889-1929.

The early yield of whitefish was high in the Ontario waters of Lake Huron proper;⁷ the average was 759,000 pounds for the 7 years, 1879-1885. The annual catch varied erratically but averaged much lower (283,000 pounds) in the period, 1886-1898. The year 1899 was the first in a long period of low production. With the exception of 1908 and 1909, for which years the accuracy of the statistics is open to question (appendix A), the take of whitefish did not exceed 100,000 pounds at any time in the years, 1899-1922 (average, 57,000 pounds). These years of low output nearly coincided with a similar period in Michigan (1897-1921). The increase to a higher level of production in 1923 in Ontario resembles the increase that occurred in the State of Michigan waters of the lake a year earlier, in 1922. The significance of the increase in 1923 is made questionable by the fact that additional waters were included under Huron proper in 1922 and later years (see footnote 7). It should be pointed out, however, that this extension of Huron proper was not accompanied by an increase in the recorded catch in 1922. Furthermore, comparisons may be made among the years, 1922-1939. Within this period the yield increased irregularly through 1935 and thereafter dropped rapidly. The take exceeded 300,000 pounds in each of the years, 1933-1935. The relatively high yields of these years were still considerably less than those of the early period (1879-1886) even though the recent figures covered more territory. Although production declined in the Ontario waters of Lake Huron proper after 1935, it was still above 100,000 pounds in 1939.

The catch of whitefish in Georgian Bay⁸ increased from an average of 1,622,000 pounds per year in 1879-1886 to an average of 4,267,000 pounds in 1887-1894. The decrease that began toward the close of the latter period brought the production of whitefish in 1895 approximately to the level about which the yield fluctuated during the 45 years, 1895-1939. The relative stability of the take in 1895-1939 is brought out by the fact that production exceeded 2 million pounds only once (1904) and fell below

⁷ Production listed in table 1 under this heading for the years, 1879-1921, is for the shore of Lake Huron from Cape Hurd at the tip of the Saugen Peninsula to the extreme southern end of the lake. Beginning in 1922, however, more northerly localities (islands of the open lake and the westerly shore of Manitoulin Island) were included in "Huron proper."

⁸ Production listed in table 1 under this heading includes the catches from the entire North Channel and Manitoulin Island regions except in 1922 and later years. (See footnote 7.)

one million pounds only 5 times (1897, 1898, 1905, 1909, and 1912) during the 45 years. The average annual production of 1895-1939 was 1,333,000 pounds. This average may be accepted as an estimate of normal production in Georgian Bay. The relatively good yields of 1933-1935 suggest an increase comparable (but less pronounced) to that which took place in the same years in the Ontario waters of Lake Huron proper. Again it may be observed that the change in the territory covered by the statistics collected after 1921 showed no effect on the figures of yield.

It may be noted here that the periods of decline and of increase in the production of whitefish in the Michigan waters were followed a year or two later by similar periods in the Ontario waters of Lake Huron. This correspondence suggests that the annual fluctuations in ecological conditions on the two sides of the lake may be similar. The changes in take in the Georgian Bay waters, however, showed no similarity with those in Lake Huron proper.

The totals for the entire lake indicate that the earlier years of the fishery were the years of the heaviest yields. Especially noteworthy was the high production in the period, 1889-1894, when the average annual catch was 6,295,000 pounds.⁹ Subsequent to 1894 the production of whitefish was relatively stable over a long period. The catch rose above 3 million pounds only once (1916) in the period, 1895-1925,¹⁰ and dropped below 2 million pounds only 5 times (1897, 1898, 1905, 1912, and 1913). The average production in this period (with the catch for 1908 omitted) was 2,351,000 pounds, which yield may be accepted as the normal for the entire lake. Good catches in both Canadian and United States waters made possible yields that were consistently above 3 million pounds in the years, 1926-1929 (average, 3,298,000 pounds). It was in the period, 1930-1934, however, that the production of the modern fishery reached its greatest heights. The take was greater than 4 million pounds in all 5 years and exceeded 5 million pounds in 3 years. The average was 5,087,000 pounds. The most recent of the earlier years with comparable production was 1893. It is to be noted that Canadian waters were largely responsible for the high production of the early years (1893 and earlier), whereas in 1930-1934 United States waters accounted for the bulk of the catch. In fact, the Canadian production exceeded that of the United States in every year except 1914, 1922, 1926, and the years, 1930-1934. By reason of a continuous decrease in production the average yield for 1935-1939 was only 2,645,000 pounds. The catch of 1,645,000 pounds in 1939 was the lowest for which there is a record. The small yield in that year can be attributed in large measure to the collapse of the fishery in United States waters.

LAKE MICHIGAN

The first acceptable records of the production of whitefish in Lake Michigan (table 1), as in the United States waters of Lake Huron, begin with the year 1889. (The 1890 record for the State of Michigan includes species other than whitefish.)¹¹ Attention will be given first to the production in the State of Michigan waters, the area with which the present report is most concerned. It is true also that the data are more complete for the State of Michigan waters than for other regions of the lake and that the production in these waters dominates the catch in the entire lake.

The production of whitefish in the State of Michigan waters of Lake Michigan was between 2 and 3 million pounds in 10 of the 19 years, 1889 and 1891-1908. (See fig. 3.) The catch was less than 2 million pounds in 6 years (less than 1½ million pounds in the 3 years, 1894-1896) and was more than 3 million pounds in only 3 years (1889, 1907, and 1908). The 1889 yield of 5,005,000 pounds was the highest for which there is a dependable record. The average for the period was 2,370,000 pounds. Production tended to decrease in the earlier span of years but to increase in the later part of the period.

⁹ It is unlikely that the inclusion of the catch of pilots in the production figures of whitefish in State of Michigan waters in 1890 affected this average materially.

¹⁰ No data for 1909-1911; the production of 3,060,000 pounds in 1908 may be discounted because of the questionable accuracy of the data for the Ontario waters of Huron proper in that year (p. 381).

¹¹ See appendix A for a discussion of the defects in the statistics for 1879 and 1885 and for the State of Michigan waters in 1890 and appendix D for the 1940-1942 records.

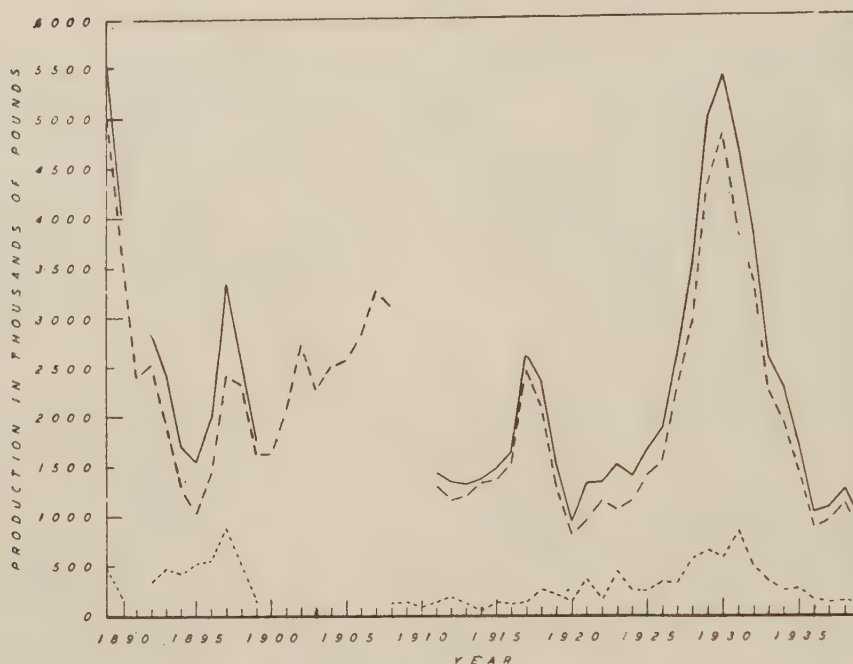


FIGURE 3.—Commercial production of whitefish in Lake Michigan, 1890-1939. Short dashes, State of Wisconsin waters; long dashes, State of Michigan waters; solid line, entire lake.

The general level of the yield was lower over the period, 1911-1926, than in 1889 and 1891-1908; the 1911-1926 average was only 1,361,000 pounds. The catch was between 1 and 1½ million pounds in 10 of the 16 years. Four years (1916, 1917, 1918, and 1926) had productions of more than 1½ million pounds (more than 2 million pounds in 1917 and 1918) and two years (1920 and 1921) had yields of less than a million pounds.

An increase in production that got under way as early as 1924 and proceeded slowly in the years, 1924-1926, became sufficiently rapid in 1927 to raise the catch above 2 million pounds. The catch continued to increase rapidly until a maximum of 4,813,000 pounds was reached in 1930. The subsequent decline did not carry the take of whitefish below 2 million pounds until 1934. The average yield for the 7 years, 1927-1933, was 3,386,000 pounds. This average was greater than the largest yield reported for any single year earlier than 1929 with the exception of 1889 and possibly of some other years prior to 1891—years for which accurate statistics are lacking.

The average production of whitefish in the most recent period, 1934-1939, was 1,191,000 pounds. The yield exceeded 1½ million pounds in only one year (1934), and in two years (1936 and 1939) it was not far above the lowest catch recorded for any previous year (806,000 pounds in 1920).

The history of the production of whitefish in the State of Michigan waters of Lake Michigan may be summarized as follows. The catch fluctuated about a level of somewhat more than 2½ million pounds during the earliest period (1889 and 1891-1908) for which reliable statistics are available; the annual yields tended to be below average and to decrease in the earlier years and to be above average and to increase in the later years of this period. The level of production was relatively low in the years, 1911-1926, with the catch exceeding 1½ million pounds in only 4 of the 16 years. The grand average of 1,909,000 pounds covering both periods (1889-1926) may perhaps be accepted as the normal yield in these Michigan waters. The years, 1927-1939, constituted a period of wide fluctuations in production that resembled the variations that took place in the State of Michigan waters of Lake Huron at about the

same time (1930-1939). Further considerations of these more recent fluctuations will be found in the next section.

The take of whitefish was relatively high in the Wisconsin waters of Lake Michigan¹² in most of the earlier years for which records are available. The catch averaged 481,000 pounds for the years, 1889-1897, and was less than 300,000 pounds in only 1 of 8 years (1890). The yield of 886,000 pounds in 1897 was the highest for which there is a record. (The statistics for 1885 include species other than whitefish.)

Statistics of the production of whitefish in the Wisconsin waters of Lake Michigan are available for only 2 of the 10 years, 1898-1907. The catches of both 1899 and 1903 were a little above 100,000 pounds and at approximately the level of production for 1908-1917. The average annual take for 12 years within the 20-year period, 1898-1917 was 116,000 pounds. In these 12 years the production exceeded 150,000 pounds only once (1912) and was less than 100,000 pounds twice (1910 and 1914).

An increase occurred in 1918 in the general level of production. The average catch of the 8 years, 1918-1925, was 256,000 pounds. Production within the period was variable and ranged from 131,000 pounds in 1920 to 443,000 pounds in 1923.

The year 1926 was the first in an 8-year period during which the output of whitefish in the Wisconsin waters of Lake Michigan did not fall below 300,000 pounds. The average 1926-1933 yield was 508,000 pounds, the maximum of 842,000 pounds in 1931 constituting the highest production since 1897. The increased catch in Wisconsin waters of Lake Michigan in 1926-1933 corresponds to the high production in the State of Michigan waters of Lakes Michigan and Huron in approximately the same general period.

The peak Wisconsin yield of 1931 was followed by a rapid if irregular decrease. The average annual production of the most recent 6-year period, 1934-1939, was 171,000 pounds. The catch of 111,000 pounds in 1939 was the lowest since 1916. Production was below the 1939 level in only 3 years (1910, 1914, and 1916) of the 42 years for which there are records in the period, 1889-1939. Probably the best estimate of the normal take of whitefish for these Wisconsin waters is the grand average for all years (1889-1939), namely, 295,000 pounds.

Despite defects (inclusion of the catches of blackfins, longjaws, and Menominee whitefish) in the whitefish statistics for the whole of Lake Michigan in 1879 and 1885 (in 1890 a separation of the catches of whitefish and of blackfins, longjaws, and pilots was possible for the entire lake but not for Michigan waters; Wisconsin data were taken from State sources) the data provide evidence, nevertheless, that the level of production of whitefish in the earlier years was considerably higher than in later years. The only information on the extent to which the whitefish statistics for Lake Michigan may have been distorted by the inclusion of the catches of blackfins, longjaws, and Menominee whitefish is provided by the data for 1890. In that year, according to the Report of the United States Commissioner of Fisheries, the catch of these three species made up 1,398,238 pounds of the reported whitefish take of 5,455,079 pounds in the entire lake. (Data were not given on the production of the species named, in the waters of the individual States.) The catch of whitefish alone (4,056,841 pounds), therefore, made up 74.4 percent of the combined output of whitefish, blackfins, longjaws, and Menominee whitefish.

If it is assumed that whitefish made up the same percentage of the reported catch in Lake Michigan in 1879 and 1885 as in 1890, the following estimates of production in these years are obtained: 1879, 8,951,000 pounds; 1885, 6,438,000 pounds. To be sure, the use of the percentage derived from statistical data for 1890 for the estimation of the catch of whitefish in earlier years is open to severe criticism. Undoubtedly, the relative abundance of whitefish and of blackfins, longjaws, and Menominee whitefish in the catch varied from year to year. Nevertheless, the preceding estimates, inexact as they may be, together with records for 1889 and 1890 provide strong evidence in support of the belief that production of whitefish in the

¹² For a discussion of Wisconsin's whitefish production in Green Bay and Lake Michigan proper separately, see appendix C.

earlier years of the fishery was greater than in 1891 and subsequent years. The normal annual output of these earlier years most probably exceeded 5 million pounds.

The description of the fluctuations in the production of whitefish in the entire lake before 1911 is made difficult by the lack of complete information in a number of years.¹³ Records of the total yield are available for only 11 years of the period, 1889-1910. These catches exhibited considerable variation. The production was less than 2 million pounds in 3 years (1894, 1895, and 1899), ranged between 2 and 3 million pounds in 4 years (1892, 1893, 1896, and 1903), fell between 3 and 4 million pounds in 2 years (1897 and 1908), and exceeded 4 million pounds in 1889 and 1890, the earliest years of the period. The average for the 11 years was 2,813,000 pounds.

The level of whitefish production for the entire lake was considerably lower in the years, 1911-1926. The catch was greater than 2 million pounds in only 2 years (1917 and 1918) of the 16, and in 10 years production was below 1½ million pounds. The 16-year average was 1,566,000 pounds.

Improved catches in both Wisconsin and Michigan waters were responsible for an uninterrupted period of 8 years, 1927-1934, in which the total catch of whitefish in Lake Michigan did not fall below 2 million pounds. The production was more than 3 million pounds in 5 of these years (1928-1932), was above 4 million pounds in 3 years (1929-1931), and exceeded 5 million pounds in 1930. The average for the 8-year period was 3,717,000 pounds. The production in each of the 3 years, 1929-1931, was greater than that recorded for any year of the period, 1890-1928, although a higher yield was recorded for 1889 and there is evidence that the catch of whitefish in certain years prior to 1889 may have been even greater.

The average annual production of whitefish in Lake Michigan in the most recent 5-year period, 1935-1939, was 1,201,000 pounds. The catches in 1936, 1937, and 1939 were all below the smallest yield recorded for any year prior to 1936 except 1920; the 1939 record provides the second report of a total whitefish catch in Lake Michigan of less than a million pounds.

The grand average of 2,074,000 pounds for the years, 1889-1926, may perhaps be accepted as the normal yield of whitefish for the entire lake.

RECENT LARGE INCREASE IN THE PRODUCTION OF WHITEFISH IN GREAT LAKES WATERS

The preceding pages were devoted exclusively to a description of fluctuations in the production of whitefish in the various waters of Lakes Huron and Michigan. A discussion of these fluctuations in terms of variations in the abundance of whitefish has been avoided deliberately because of the many disturbing factors that render such interpretations exceedingly unreliable.

A fundamental difficulty in the use of the statistical data of the type given in table 1 for estimations of fluctuations in the abundance of fish lies in the lack of adequate information on the intensity of the fishery. It is known that in general the fishing intensity of the early fishery was far less than that of the modern fishery—that with the passage of the years the number of men and boats engaged in commercial operations increased greatly. It is known too that certain technical developments such as the invention of power lifters, improvements in the efficiency of nets, and the construction of faster and more cheaply operated craft, permitted an expansion of fishing activity out of proportion to the mere increase in men and boats. Because of the known increase in fishing intensity a given annual catch in the earlier years of the fishery may be held to indicate a greater abundance of fish than an equally large production a number of years later.

Changes in fishery regulations also may affect production significantly. Increases or decreases in the minimum legal mesh size, the imposition of a closed season, the establishment or abandonment of a fishery for spawn, the closure of grounds or the restriction of operations in certain areas, changes in the size limit of fish—all these

¹³ Totals were omitted for all years in which records were lacking for either the State of Michigan or the State of Wisconsin waters. Certain of the totals listed for Lake Michigan in table 1 do not include the production in Illinois and Indiana waters, but the omission of these catches most probably had little effect on the values of the totals. (See appendix A.)

and other changes in fishery regulations can have a profound if undeterminable effect on total yields.

Production may vary according to general economic conditions. In periods of depression low prices may render operations unprofitable and thus bring about a curtailment of fishing activities. On the other hand, an economic depression has been observed in at least one industrial district to have the reverse effect of stimulating fishing intensity. Here numbers of unemployed turned to small-scale fishing as an emergency source of income—meager, to be sure, but preferable to none at all.

Other factors, such as weather conditions, might be listed which cause fluctuations in production that are independent of the level of abundance of the stock. However, those mentioned are sufficient to bring out the difficulties inherent in the use of catch statistics for the estimation of changes in the abundance of fish, particularly over long periods of time.

Despite the limitations just outlined, there is good reason to believe that under normal conditions (without disruption in the methods or regulations of the fishery). over limited areas, and for short periods of years, large increases or decreases of production may serve as reliable indicators of increases or decreases in the abundance of fish on the grounds. The changes in annual yields do not measure the changes in abundance, but merely indicate their occurrence. This view concerning the general relationship between the production and abundance of fish has grown from the careful examination of records that have been maintained, beginning in 1929, of the annual fluctuations in the catch and abundance of fish on the grounds and in the intensity of the fishery for all commercially important species in 21 fishing areas of the State of Michigan waters of the Great Lakes.

Ordinarily fluctuations in production exceed those in abundance; that is, the increases in the catch tend to be relatively greater than the increases in abundance when the latter rises above the average, and conversely, the decreases in the yields tend to be greater than the decreases in abundance when the latter falls below the average. As a result the curves of production often are "exaggerations" of the curves of abundance. This general relationship between abundance and catch has its origin in the circumstance that fishing intensity tends to be above average when abundance is above average and below when abundance is below. Of course, exceptions occur in the relationships outlined above but these exceptions do not affect the general validity of the statements.¹⁴

Among the increases in production that safely may be held to reflect (but not measure) a greater abundance of fish on the grounds are those that occurred in the catch of whitefish in Great Lakes waters near the beginning of the 1930's. Although the actual years of high yields varied somewhat in the different waters, an increase occurred in every important center of production. The increase in the catch was relatively greater in the State of Michigan waters of Lake Huron than in other areas.

The extent to which the recent increase in production was relatively greater in the State of Michigan waters of Lake Huron than in other areas may be brought out by comparisons of the take in the 2 or 3 recent years of greatest yield with the average catch over a period of earlier years. The average production in the peak years, 1931 and 1932, was 3.67 times the average for the years 1889 and 1891-1929. This value is considerably higher than the ratios for other areas as the following tabulation shows:

Area	Years of early period	Years of recent period	Ratio of recent to early production
Huron (State of Michigan).....	1889, 1891-1929	1931-1932	3.67
Huron (Province of Ontario-Huron proper).....	1893-1932	1933-1935	2.86
Huron (Province of Ontario-Georgian Bay, North Channel).....	1895-1932	1933-1935	1.26
Michigan (State of Michigan).....	1889, 1891-1926	1929-1930	2.38
Michigan (State of Wisconsin).....	1889-1927	1929-1931	2.58
Superior (State of Michigan).....	1911-1930	1931-1933	1.97
Erie (entire lake).....	1921-1927	1929-1931	1.68

¹⁴ See part II for a discussion of the relationships among the fluctuations in the production and abundance of whitefish and in the intensity of the whitefish fishery in Lakes Huron and Michigan.

Although the selections of the periods for the preceding comparisons, based on the examination of the statistical data, were to a certain extent arbitrary, reasonable changes in the years included in these periods would not affect the validity of the general conclusion that the increase in the production of whitefish was greater in the State of Michigan waters of Lake Huron than in other Great Lakes areas.

Despite the known risks involved in the estimation of changes in abundance from changes in production, the ratios of the preceding paragraph would suggest the possibility that the recent increase in the abundance of whitefish may have been somewhat higher in the Michigan waters of Lake Huron than in other Great Lakes areas. Information from other sources, however, proves that such an assumption would be utterly invalid. The higher production in the Michigan waters of Lake Huron (as compared to other waters) was made possible by the introduction of a new and marvelously efficient gear, the deep trap net. The use of this net made possible a tremendous increase in fishing intensity. No doubt an increase in catch would have taken place without the use of deep trap nets; however, it was deep-trap-net operations that accounted for the relatively greater heights of production attained in the Michigan waters of Lake Huron.

The description of the annual fluctuations in the yields and abundance of whitefish and in the intensity of the whitefish fishery in the Michigan waters of Lakes Huron and Michigan, 1929-1939, presented in part II, is concerned largely with the effects of deep-trap-net operations on the fishery. It is shown that the widespread use of deep trap nets in Lake Huron (the gear was fished much less extensively in Lake Michigan) led to a multiplication of fishing intensity that raised production far beyond a reasonable level and was responsible for the subsequent collapse of the fishery.

PART II

FLUCTUATIONS IN THE PRODUCTION AND ABUNDANCE OF WHITEFISH AND IN THE INTENSITY OF THE WHITEFISH FISHERY IN THE STATE OF MICHIGAN WATERS OF LAKES HURON AND MICHIGAN, 1929-1939

INTRODUCTION

In the proper administration of commercial fisheries it is of primary importance to have at hand statistical data that afford a reliable indication of changes in the abundance of the commercially available stocks of the leading species. These data must include a record not only of the quantity of fish taken, but also of the extent of the fishing operations that led to the reported catch. Obviously, a decrease in production cannot be held with certainty to represent a depletion of the stock unless it can be demonstrated that this lowered yield has not resulted from a reduction of fishing intensity. On the other hand, an increase in catch with its suggested danger of possible overfishing may not be the result of an expansion of fishing activities but may originate in an increase in the abundance of fish on the grounds. Nor can it be said that a sustained production over a period of years demonstrates a corresponding stability of abundance, for abundance may decline or increase greatly while compensating fluctuations of fishing intensity hold the total catch at a nearly constant level. The true condition of the fisheries, therefore, cannot be measured accurately by statistics of catch alone, but should be expressed in terms of production in relation to fishing intensity, that is, catch per unit of fishing effort.

It was with a view toward obtaining complete and reliable information on the fisheries of the Great Lakes waters under the jurisdiction of the State of Michigan that the senior author devised and recommended to the Michigan Department of Conservation the monthly report system now in effect. Under this system all licensed commercial fishermen must submit each month a complete record of their daily fishing activities. The required data on each day's fishing include: fishing locality; kind and amount of gear fished; the length of time (number of nights out) stationary gear fished before it was lifted; and the catch in pounds of each species taken. From these data it is possible to determine both the yield and the intensity of the fishery.

The law requiring the submission of monthly reports became effective in September 1927. The early returns were incomplete and the individual reports were often faulty. By the beginning of 1929, however, the fishermen had obtained sufficient experience in making out their reports so that almost all returns contained the complete data necessary for statistical analysis. These records for the 11-year period, 1929-1939, comprise the basic materials on which part II of this paper is founded.

METHODS OF ANALYSIS

Methods proposed for the analysis of Great Lakes fishery statistics were described by Hile and Duden (1933).¹⁵ In general, the procedure outlined in this publication has proved satisfactory, although subsequent experience has shown certain simplifications of the original methods to be valid. (See discussion under "Units of Fishing Effort" in this section.) As an addition to the original procedure, methods have been devised for a more precise statement of changes in abundance and fishing intensity.

STATISTICAL DISTRICTS

Statistical tabulations and analyses have been made separately for six areas in Lake Huron and eight in Lake Michigan. (The boundaries of the different districts are indicated in the accompanying chart, fig. 4.) It was attempted to make these dis-

¹⁵ Hile, Ralph and William R. Duden. Methods for the Investigation of the Statistics of the Commercial Fisheries of the Great Lakes. *Trans. Am. Fish. Soc.*, vol. 63, 1933, pp. 292-305.



FIGURE 4.—Map showing the statistical districts of the State of Michigan waters of Lakes Huron and Michigan.

tricts natural divisions from the standpoint of both fishing grounds and fishing operations.¹⁶ For some purposes the data for the separate districts have been combined to provide more general information for different regions of the lakes and for the entire lakes. For convenience, the districts will be designated in later discussions by the initial letter of the lake and the number of the district. For example, the third district of Lake Huron will be termed H-3, the fifth district of Lake Michigan, M-5,***.

PRODUCTION

The production was tabulated according to gear for each month. The only important gears used for the taking of whitefish are the large-mesh gill net (4½ inches or larger, stretched measure), the deep trap net, and the pound net. The discussion in this paper will be concerned chiefly with annual totals of the catch of the different gears and of all of them combined. Data on monthly yields will be confined to the discussion

¹⁶ Hile and Duden (*loc. cit.*) stated that Lake Michigan had been divided into 11 statistical districts. Experience revealed, however, that certain of the original tentative divisions were not practical. Changes of boundaries and combinations of areas have reduced the number of statistical districts in Lake Michigan to eight. The six statistical districts of Lake Huron all proved satisfactory as originally defined.

of the effects of the deep trap net on the seasonal trend of production in Lake Huron (p. 332).

UNITS OF FISHING EFFORT

The units of fishing effort employed in this paper are:

Gill nets.—The lift of 10,000 linear feet of net (10,000 foot-lifts).¹⁷

Impounding nets (deep trap nets and pound nets).—The lift of one net (1 net-lift).

Fishing effort may be expressed as total effort and as effective effort (with respect to a given species). In large-mesh gill nets, for example, the total effort for a given area over a certain interval of time is the total number of units of 1,000 feet (see footnote 17) of net lifted. The effective effort with respect to whitefish is the number of units of gill net lifted that actually took this species. Corresponding definitions of total and effective effort apply to the pound net. A distinction between total and effective effort is necessary because both large-mesh gill nets and pound nets are fished for other species on grounds where whitefish do not occur. In the deep trap net, which was designed and operated primarily for the capture of whitefish, the total fishing effort and the effective effort with respect to this species may be considered identical. All tabulations of catch per lift in this paper are based on effective fishing effort.

In addition to the above "units of effort," the methods proposed by Hile and Duden defined "units of intensity" which included a consideration of fishing time (nights out). The intensity unit for gill nets was defined as the fishing effort of 1,000 feet of gill net over a period of one day, and for impounding nets as the fishing effort of one net over a period of one day. The basis for these definitions of intensity units was the assumption that the amount of fishing done by stationary gear varies directly with the time out. This assumption holds, for example, that a net which is out three nights may be expected to take three times as many fish as the same net in one night.

Subsequent detailed analyses of hundreds of fishermen's reports made by Hile and described briefly by him in 1935¹⁸ and by Van Oosten (1935)¹⁹ have proved this preliminary assumption to be erroneous. Although the catches of both gill nets and impounding nets, on the average, become larger with increase in fishing time, the improvement in the catch is far less than might be expected on theoretical grounds. A summary of the data on the actual relationship between fishing time and the average size of the lift in the gears most important in the whitefish fishery appears in table 2. In this table all catches are expressed as percentages of the catch of nets one night out. Although the data for the three gears disagree somewhat as to the relationship between the actual size of the catch and the number of nights out, these small discrepancies lose significance in the face of the large deviations that all the actual catches show with respect to the theoretical catches. For example, the largest increase in nets 2 nights out over nets 1 night out (pound nets) was only 16 percent of the expected increment of 100. Similarly, the largest increase in the catch of nets 5 nights out over 1 night out (54 in pound nets) was only 13.5 percent of the expected increment of 400. It is obvious, therefore, that only small increases in the catch can be expected as the time between lifts is increased. Consequently, the use of the catch per net per night as a measure of abundance is not valid. The strictly valid unit for the measure of abundance is neither the catch per lift nor the catch per night, but is rather the catch per lift, corrected for fishing time (from empirical data of the type contained in table 2).

The necessity for considering fishing time in the computation of annual fluctuations in abundance depends, of course, on the existence of annual variations in the average number of nights out. Annual variations in fishing time occur in all areas and for all stationary gears, but for a single area and a single type of gear these variations have a limited and characteristic range. The limited range of variation in the average number of nights out, together with the fact that a change in fishing time affects the

¹⁷ The unit of effort was defined originally as the lift of 1,000 feet of gill nets. In the present study, however, the catch of gill nets has been recorded in terms of the yield per 10,000 foot-lifts (tables 11 and 17) in order to obtain values more nearly comparable with the catch per unit of effort of pound nets and deep trap nets.

¹⁸ The Fisherman, vol. 4, no. 12, pp. 1 and 2, 1935.

¹⁹ Van Oosten, John. Logically Justified Deductions Concerning the Great Lakes Fisheries Exploded by Scientific Research. Trans. Am. Fish. Soc., vol. 65, 1935, pp. 71-75.

TABLE 2.—*Relationship between fishing time and the average size of the lift*

[In order that the data for the different gears may be comparable, the catch per lift at one night out is set at 100 and all other catches expressed as percentages of this value. In parentheses, the number of fishermen's reports upon which determination was based]

Item	Number of nights out				
	1	2	3	4	5
Theoretical catch.....	100	200	300	400	500
Actual catch.....	100	111	120	133	150
		(304)	(430)	(403)	(278)
	100	115	116	128	126
		(157)	(228)	(272)	(197)
	100	116	138	141	154
		(353)	(458)	(306)	(177)

¹Less than preceding catch.

size of the catch only slightly, suggested the possibility that abundance curves calculated from the average catch per lift without reference to time might differ only slightly from curves calculated from the average catch per lift, corrected for time. To test this possibility a series of abundance curves for the period, 1929–1934, was computed by each of the two methods, covering all types of stationary gear and a variety of species and fishing areas. For each gear particular care was taken to select the statistical district with the widest annual variation in the average fishing time. Despite this selection, in each example the two curves resembled each other so closely that the same conclusions concerning the annual changes in abundance would have been drawn from either of them. As the neglect of the time element does not affect the results materially, all computations of abundance have been based on the catch per lift, without reference to time.

ESTIMATION OF ABUNDANCE AND FISHING INTENSITY

The method employed for the estimation of the abundance of species of fish in the State of Michigan waters of the Great Lakes in different calendar years was outlined by Hile (1937).²⁰ The definition of fishing intensity was given by Hile and Jobes (1941).²¹ The steps in the determination of the general abundance of a species within a fishing area (statistical district) in a particular calendar year are:

(1) The "expected catch" of each important gear is determined as the product of known fishing intensity (number of impounding nets or thousands of feet of gill nets, that took the species, lifted within the district during the entire 12 months) and the average catch of that species per unit of fishing effort over a period of years.

(2) The expected catches as determined individually for the important gears are added to obtain the "total expected catch."

(3) The "general abundance" is the actual catch of the important gears expressed as a percentage of the total expected catch of the same gears.

As the average catch per unit of effort is constant in all of the computations of expected catch for a single type of gear, annual fluctuations in the expected catch by each gear and hence for all gears combined depend only on the amount of gear lifted. Consequently, the total expected catch of any single year, expressed as a percentage of the average total expected catch over a period of years, provides a measure of the relative intensity of the fishery in that particular year.

The above procedures make it possible to combine the data for all gears important for the capture of a particular species in such a way as to obtain estimates of the "general" abundance and of the total fishing intensity.

Originally all estimates of abundance and fishing intensity were made with reference to average conditions over the 6-year period, 1929–1934. Later, the percentages were adjusted to describe deviations about the mean for the 11 years, 1929–1939.

²⁰ Hile, Ralph. The Increase in the Abundance of the Yellow Pike-Perch, *Stizostedion vitreum* (Mitchill), in Lakes Huron and Michigan, in Relation to the Artificial Propagation of the Species. Trans. Am. Fish. Soc., vol. 66, (1936) 1937, pp. 143–159.

²¹ Hile, Ralph and Frank W. Jobes. Age, Growth, and Production of the Yellow Perch, *Perca flavescens* (Mitchill), of Saginaw Bay. Trans. Am. Fish. Soc., vol. 70, (1940) 1941, pp. 102–122.

GENERAL REMARKS

It does not come within the province of this paper to undertake a detailed criticism of the statistical methods employed here, to discuss at length possible sources of systematic errors, to attempt to estimate the degree of reliability of certain necessary approximations, or to explain the basis for the selection of methods followed over possible alternative procedures. It can be said only that the methods employed for the analysis of the statistics of the commercial fisheries of the Great Lakes have been developed gradually from a careful study of extensive data covering all the commercially more important species over a period of years and in a large number of different localities. These methods have been adapted specifically to conditions in the Great Lakes. An outstanding feature of the Great Lakes fisheries is that most species are taken in quantity by several types of gear and that most types of gear take several species (usually simultaneously). These circumstances add greatly to the complexity of the problem of analysis.

No claims are advanced for the indexes of abundance and fishing intensity as "precision measures" of the changes that occurred in the fishery. On the other hand, we believe them to be sufficiently sensitive to bring out all changes of significant magnitude. This belief is supported by the consistency with which conclusions based entirely on our statistical data have been corroborated by reliable evidence gained independently from other sources (interviews with fishermen; observations of field workers).

Although, as stated previously, a general criticism of our methods of analysis will not be undertaken, it does appear desirable to call attention to certain difficulties of interpretation peculiar to the statistics of the whitefish fishery.

It is indeed unfortunate that the statistical data on the commercial fishery for whitefish are less satisfactory than those for any other important commercial species. The invention and rapid expansion in the use of that tremendously efficient gear, the deep trap net, brought about, particularly in Lake Huron, an almost immediate threat of depletion or commercial extinction to the whitefish stocks of the areas in which the net was fished. In this critical situation the need for dependable statistical measures of abundance was most pressing. However, the very circumstances that made the need for adequate statistical data so urgent also made the interpretation of these data difficult. The chief obstacles to appraising the statistical data on the whitefish over the period, 1929-1939, are: lack of information concerning normal conditions, inaccurate data on the deep-trap-net fishery, and the difficulty of bridging the transition to a fishery dominated by this gear.

As stated earlier (p. 314), in the statistical study of the important commercial species in the State of Michigan waters of the Great Lakes, the average conditions of production, abundance, and fishing intensity during the 6-year period, 1929-1934, were employed tentatively as the point of reference for the study of fluctuations. The fisheries for most species appeared to be approximately normal (with reference to modern conditions) during this period; consequently the 6-year averages may be expected to provide a fairly reliable basis for estimating changes in the condition of the fisheries, not only in that period but in subsequent years as well.

The whitefish fishery, however, was not normal in the years, 1929-1934, nor can the average conditions in the longer period, 1929-1939, be held to provide a satisfactory point of reference. It is recognized generally that whitefish were abnormally abundant at the beginning of these periods. The peak of abundance probably was reached in Lake Michigan in 1929 and in Lake Huron a year or so later. The high abundance in turn stimulated fishing intensity. As a result, production, abundance, and fishing intensity were all doubtless far above normal in the earlier years of the period for which detailed statistics are available. It should then be kept in mind throughout the discussion of the following sections that all fluctuations are described with reference to averages, the relationship of which to the normal is not known.

The interpretation of the Lake Huron data is made even more difficult by the disturbing effects of the use of the deep trap net. This gear, which became the dominant one for the capture of whitefish as early as 1931, raised production to excessive heights and disrupted completely the ordinary course of return to normal conditions.

The fact that in all districts but H-2 the deep trap net was not fished throughout the entire "period of reference" (1929-1934) introduced certain difficulties into the estimation of abundance. For example, the deep trap net was operated in H-1 during only 5 years (1930-1934) of this 6-year period. The average catch of whitefish per lift of deep trap nets in the years, 1930-1934, was 111.08 pounds. However, the data for large-mesh gill nets and pound nets indicated that the 1930-1934 abundance averaged only 99.12 percent of the 1929-1934 mean. Consequently, the average catch per lift of deep trap nets would have been higher had the gear been fished in 1929 also. It was necessary, therefore, to base the computations of the expected catch (p. 314) of deep trap nets on the "corrected" catch per lift, $111.08/0.9912=112.07$ pounds.

Although this method of "correcting" the average catch per lift of deep trap nets (in some districts the data for pound nets had to be treated similarly) is sound logically, the actual reliability of the results is open to question in some districts in which the rise of the deep-trap-net fishery was accompanied by the practical extinction of the gill-net and pound-net fisheries (for whitefish). The correction was based, for example, on the data for only 3 years in H-3 and H-5 and for 2 years in H-6. The difficulties involved in following annual changes in abundance in areas in which the deep trap net replaced other types of gears completely or nearly completely will be mentioned again on page 328.

The deep trap net was important also in Green Bay and northern Lake Michigan, but the disturbance of the fishery was not as severe as in Lake Huron.

Although the greatest need for dependable statistical data existed with respect to those districts in which the deep trap net became almost the only gear that produced whitefish, it was for precisely these areas that the original data were least trustworthy. This lack of dependability had its origin in the extensive inaccuracies and misstatements of fact known to have occurred in the reports of numerous deep-trap-net fishermen. This observation is not intended as an indictment of any fisherman or group of fishermen. Nevertheless, the fact that these inaccuracies existed cannot well be ignored. To discuss changes in abundance computed from deep-trap-net data without giving some idea as to their degree of dependability would be misleading. Misstatements were found in the reports of deep-trap-net fishermen as to the type of gear fished, the numbers of nets lifted, and the size of the catch.

Numerous deep-trap-net reports were indicated erroneously to be reports of pound-net operations. Most of the errors of this type were made by operators in the Saginaw Bay region in 1931 and in both the Saginaw Bay and Harbor Beach regions in 1932. In other years and in other districts the designation of deep trap nets as pound nets was much less frequent. Without naming sources of information or explaining the procedure followed, it may be stated that we are certain that we have detected and corrected practically all, if not all, of the misstatements as to the type of gear. Consequently, this originally serious source of error does not affect materially the data of this paper.

It has not been possible to correct the inaccuracies of data as to the number of nets lifted and the size of the catch, nor is there any basis for a good estimate of the extent of these inaccuracies. Where there was opportunity of comparing actual and reported data the discrepancies were sometimes appalling. Some fishermen not only reported incorrectly the number of nets lifted but gave dates of lifting that did not coincide with the dates on which they actually left port. The reported catches were often understated. The extreme in this type of misrepresentation is offered by the report of an operator who is known to have taken more fish in a single day than he reported for the entire month. It must be considered highly probable that the actual total production of whitefish in deep trap nets was far above that recorded in this study.

In calling attention to the defects in the deep-trap-net data it is not intended to imply that all operators of deep trap nets submitted erroneous and carelessly prepared reports. There is good evidence that many of them prepared scrupulously accurate accounts of operation and of catch. Although the number of inaccurate reports may be sufficient to invalidate the deep-trap-net data as descriptive of details, these data still serve satisfactorily to indicate the trends of the fisheries in the different districts. This view finds support in the fact that for the whitefish as well as for other species there

was good agreement between conclusions as to the course of the fishery based on statistical data and on the testimony of the fishermen themselves.

WHITEFISH FISHERY OF LAKE HURON, 1929-1939

In part I attention was called to the general increase in the abundance and production of whitefish that occurred in the waters of the Great Lakes in the late 1920's and early 1930's. Emphasis was placed on the fact that the increase in yield in Michigan waters of Lake Huron was relatively much higher than in other waters. The average Michigan catch in Lake Huron in the two peak years, 1931 and 1932, was 3.67 times the average annual production over a period of earlier years, and the years 1930, 1933, 1934, and 1935 had yields well above normal, whereas in other waters the average annual productions during the recent maximum were only 1.26 to 2.86 times the earlier averages (p. 309). The excessive catch in Lake Huron was attributed to the widespread use of the deep trap net in that lake. The detailed data that will be presented for the six statistical districts in the State of Michigan waters of Lake Huron fully support this earlier position. In fact, the origin and expansion of the deep-trap-net fishery dominate the recent history of Michigan's whitefish fishery of Lake Huron so completely that a summary of the 1929-1939 statistics constitutes in reality little more than a study of the effects of this new gear.

The deep trap net was introduced into Lake Huron off Alpena, Mich., in district H-2 in July 1928, and continued to be fished in the same area in 1929. The rapid expansion of the deep-trap-net fishery got under way in 1930. In this year the net was fished extensively not only in the neighborhood of Alpena but also in H-1 (especially in Hammond Bay) and in H-3 (mostly from Au Sable-Oscoda); a few deep trap nets were used also in 1930 on the "Middle Grounds" off Saginaw Bay (H-4). No new statistical districts were added to the deep-trap-net grounds until 1932, in the latter part of which season the net was introduced into the waters of southern Lake Huron off Harbor Beach (H-5). The expansion into H-6 in 1933 completed the coverage of the Michigan waters of the lake. This sequence makes the history of the deep-trap-net fishery, in a sense, discontinuous as the major "scene of action" shifted from year to year.

FLUCTUATIONS IN THE PRODUCTION OF WHITEFISH IN LAKE HURON

The production of whitefish in Lake Huron²² increased phenomenally in 1930 and 1931 (table 3). The catch of 2,879,000 pounds in 1930 was nearly twice the 1929 yield of 1,456,000 pounds, and the 1931 production of 4,140,000 pounds represented an additional increase of 1,260,000 pounds above the 1930 level. The decline from the 1931 yield was relatively insignificant in 1932 (decrease of 89,000 pounds). The reduction in the catch was large, however, in the succeeding years, averaging 719,000 pounds per year for the 3 years, 1933-1935, 446,000 pounds for the 3 years, 1936-1938, and 303,000 pounds in 1939. Despite these large decreases the catch did not return to an approximately normal level until 1936. The subsequent declines carried the production far below normal. The 1938 yield of 558,000 pounds was only a little above the lowest catch recorded for any previous year (555,000 pounds in 1900), and the 1939 production of only 255,000 pounds was less than half the previous all-time low. The 11-year period (1929-1939) saw, therefore, a remarkable cycle in the yield of whitefish in Lake Huron. From a nearly normal level in 1929 the catch increased suddenly to the unprecedented height of more than 4 million pounds in 1931 and 1932 only to decline rapidly to an unprecedented low yield in 1939.

Much of the increase to the 1931-1932 peak and of the high production in 1933-1935 can be traced to the new gear, the deep trap net. The catch by this gear jumped from 87,000 pounds in 1929 to 871,000 pounds in 1930 (a ten-fold increase), 2,080,000 pounds in 1931, and 2,764,000 pounds (the peak production for the gear) in 1932. The catch of deep trap nets did not fall below 2 million pounds in the 4 years, 1931-1934.

²² In this and the following section the terms, "Lake Huron" and "the entire lake," refer to the State of Michigan waters only.

TABLE 3.—*Production of whitefish in pounds according to gear in the State of Michigan waters of Lake Huron, 1929–1939*

[Percentages of annual yield in parentheses]

Year	Production in gear				Total annual production	Increase or decrease
	Large-mesh gill net	Deep trap net	Pound net	Other		
1929-----	{ 489,961 (33.6)	{ 87,121 (6.0)	{ 823,696 (56.6)	{ 55,590 (3.8)	1,456,368	—12,433
1930-----	{ 613,752 (21.3)	{ 871,321 (30.3)	{ 1,302,586 (45.2)	{ 91,781 (3.2)	2,879,440	1,423,072
1931-----	{ 619,515 (15.0)	{ 2,079,596 (50.2)	{ 910,940 (22.0)	{ 1529,721 (12.8)	4,139,772	1,260,332
1932-----	{ 385,566 (9.5)	{ 2,764,317 (68.2)	{ 569,698 (14.1)	{ 1330,753 (8.2)	4,050,334	—89,438
1933-----	{ 269,271 (8.1)	{ 2,704,576 (81.1)	{ 305,229 (9.2)	{ 54,825 (1.6)	3,333,901 ¹	—716,433
1934-----	{ 189,701 (7.4)	{ 2,061,483 (80.3)	{ 258,207 (10.0)	{ 58,842 (2.3)	2,568,233	—765,668
1935-----	{ 132,789 (7.0)	{ 1,487,342 (78.5)	{ 172,280 (9.1)	{ 102,396 (5.4)	1,894,807	—673,426
1936-----	{ 88,951 (6.2)	{ 1,166,707 (80.9)	{ 127,100 (8.8)	{ 59,411 (4.1)	1,442,169	—452,638
1937-----	{ 49,937 (4.9)	{ 834,164 (81.9)	{ 107,221 (10.5)	{ 27,359 (2.7)	1,018,681	—423,488
1938-----	{ 55,677 (10.0)	{ 423,073 (75.8)	{ 58,813 (10.5)	{ 20,406 (3.7)	557,969	—460,712
1939-----	{ 41,072 (16.1)	{ 178,517 (70.0)	{ 28,911 (11.3)	{ 6,683 (2.6)	255,183	—302,786
Average-----	{ 266,927 (12.4)	{ 1,332,565 (62.1)	{ 424,062 (19.8)	{ 121,615 (5.7)	2,145,169	-----

¹ A considerable portion of this catch, entered in the original records under the heading, "Gear unknown," was taken by deep trap nets.

It cannot be concluded that all of the production of deep trap nets represented additional demands on the whitefish stock of Lake Huron or that an increase in yield would not have taken place after 1929 without the operation of this gear. Substantial increases occurred in the production of whitefish by both gill nets and pound nets in 1930, and the 1931 catch in these gears was above the 1929 level. Unquestionably the output of gill nets and pound nets would have been even higher in 1930 and 1931 and the subsequent decline in production in those two gears would have been less rapid had not considerable numbers of fishermen abandoned the use of gill nets and pound nets in favor of the much more efficient deep trap net. On the other hand, the fact that deep trap nets produced more whitefish in every year of the 5-year period, 1931–1935, than did all gears combined in 1929, and did so, as will be shown later (p. 330) in the face of a rapid decline in abundance after 1931, suggests that this gear possesses capabilities for the capture of whitefish far greater than can be attributed to either gill nets or pound nets. (Superiority of deep trap nets over pound nets is due largely to the greater range of fishing depths of the former. See pp. 331 and 332.) Although the deep trap net cannot be held to be solely responsible for the increase in production that took place after 1929, the conclusion is justified, nevertheless, that the increase would have been much smaller had this gear not been fished.

The superiority of the deep trap net for the capture of whitefish is indicated strongly by the speed with which it replaced other gears. In 1929 deep trap nets accounted for only 6.0 percent of the total yield of whitefish in Lake Huron. Two years later in 1931 they took more than half the total and by 1933 were responsible for more than 80 percent of the catch. Deep-trap-net production as a percentage of the total yield fluctuated about the 80-percent level for 5 years (1933–1937) and declined only with the virtual collapse of the fishery in 1938 and 1939.

The deep trap net became at some time the dominant gear for the capture of

whitefish in every statistical district of Lake Huron (table 4 and appendix B). With the increase in the use of deep trap nets the operations with pound nets and gill nets declined in most districts to the point of insignificance. Only in H-1 did the deep trap net fail to become established as the overwhelmingly dominant gear. The percentage of the total production of whitefish taken by deep trap nets was not greater than 38 percent in that district before 1935, and exceeded 50 percent in only 3 years (1936, 1937, and 1939). In other districts the deep trap net accounted for more than 50 percent of the total catch of whitefish in the first or second year of operation (possible exception in H-4 where considerable quantities of whitefish taken by deep trap nets in 1931 are included in the catches for which the records of gear were not available) and maintained a dominant position with great consistency throughout the later years. This statement is true especially for southern Lake Huron (H-5 and H-6 combined) where the deep trap net was responsible for more than 90 percent of the total yield in every year after 1932 and for more than 95 percent in every year after 1935.

TABLE 4.—*Production of whitefish in pounds in deep trap nets in Lake Huron, 1929-1939*

[In parentheses, the deep-trap-net production expressed as a percentage of the total whitefish production]

District or area	Production of whitefish in deep trap nets in year											Total
	1929	1930	1931	1932	1933	1934	1935	1936	1937	1938	1939	
H-1.....		{ 286,453 (37.9)	375,122 (38.0)	170,313 (27.3)	64,251 (17.6)	104,699 (27.7)	163,465 (43.8)	346,821 (64.1)	236,196 (73.2)	73,184 (40.6)	73,406 (52.0)	1,893,910 (37.2)
H-2.....	{ 87,121 (31.7)	358,872 (60.4)	376,887 (78.7)	94,527 (80.5)	28,540 (50.3)	44,153 (47.4)	94,584 (80.0)	46,602 (83.8)	14,009 (67.3)	34,315 (83.0)	41,980 (99.3)	1,221,590 (64.5)
Northern Lake Huron (H-1 and H-2).....	{ 87,121 (13.4)	645,325 (47.8)	752,009 (51.3)	264,840 (35.7)	92,791 (22.0)	148,852 (31.6)	258,049 (52.5)	393,423 (65.9)	250,205 (63.4)	107,499 (48.5)	115,386 (62.9)	3,115,500 (44.6)
H-3.....		{ 157,248 (63.5)	395,230 (84.0)	85,236 (62.0)	9,912 (70.1)	12,558 (87.2)	7,964 (89.4)	7,567 (94.5)	1,934 (69.1)	8,910 (97.2)	277 (49.7)	686,836 (67.9)
H-4.....		{ 68,748 (6.6)	1,932,357 ¹ (47.9)	1,934,325 (78.5)	620,125 (81.4)	116,849 (59.9)	138,446 (65.1)	75,438 (58.6)	121,796 (78.5)	38,224 (68.4)	18,785 (72.4)	4,065,093 (53.8)
Central Lake Huron (H-3 and H-4).....		{ 225,996 (17.5)	1,327,587 ¹ (54.9)	2,019,561 (77.7)	630,037 (81.2)	129,407 (61.8)	146,410 (66.1)	83,005 (60.7)	123,730 (78.4)	47,134 (72.5)	19,062 (71.9)	4,751,929 (55.4)
H-5.....				{ 479,916 (93.5)	1,658,753 (98.9)	783,606 (99.9)	272,746 (99.8)	119,103 (100.0)	66,688 (99.8)	41,832 (99.8)	12,247 (100.0)	3,434,891 (92.4)
H-6.....					{ 322,995 (70.3)	999,618 (90.6)	810,137 (89.1)	571,176 (96.9)	393,541 (98.5)	226,608 (98.7)	31,822 (96.1)	3,355,897 (77.7)
Southern Lake Huron (H-5 and H-6).....				{ 479,916 (67.7)	1,981,748 (92.8)	1,783,224 (94.5)	1,082,883 (91.6)	690,279 (97.4)	460,229 (98.7)	268,440 (98.9)	44,069 (97.2)	6,790,788 (84.5)
Lake Huron (all 6 districts).....	{ 87,121 (6.0)	871,321 (30.3)	2,079,596 (50.2)	2,764,317 (68.2)	2,704,576 (81.1)	2,061,483 (80.3)	1,487,342 (78.5)	1,166,707 (80.9)	834,164 (81.9)	423,073 (75.8)	178,517 (70.0)	14,658,217 (62.1)

¹ Pounds and the corresponding percentage are too low; the total production in H-4 in 1931 and 1932 included considerable quantities of whitefish for which records of the gear of capture were lacking, but a large part of which came from deep trap nets. Other totals and percentages in the computation of which these figures were involved were affected relatively less severely.

A peculiar feature of the production of whitefish in Lake Huron, 1930-1935, lay in the circumstance that a high level of yield was maintained by a successive rather than a simultaneous exploitation of the stocks in the various portions of the lake (table 5 and appendix B). In each area the catch of whitefish followed a typical cycle after the introduction of the deep trap net. Production was raised to tremendous heights for about 2 years, only to fall away sharply. Since the use of the deep trap net spread gradually throughout the lake, first one area and then another bore the burden of heavy fishing.

Although the deep trap net was fished in H-2 in 1929 (in 1928 also), it did not produce large quantities of fish until 1930. In this same year the net was employed extensively in H-1 and H-3 also and was introduced into H-4. In 1931 high yields were obtained in each of these first four districts. Thus it was possible for the production of whitefish in Lake Huron to increase phenomenally in 1930 and attain a

TABLE 5.—*Total annual production of whitefish in pounds in the different districts and areas of the State of Michigan waters of Lake Huron, 1929-1939*

[Each total is expressed also as the percentage (in parentheses) of the production of the entire lake]

District or area	Total whitefish production in year											Average
	1929	1930	1931	1932	1933	1934	1935	1936	1937	1938	1939	
H-1-----	{ 375,577 (25.8)	¹ 2755,362 (26.2)	² 987,466 (23.8)	623,670 (15.4)	364,683 (11.0)	378,105 (14.7)	372,874 (19.7)	541,392 (37.5)	373,755 (36.7)	180,127 (32.3)	141,051 (55.3)	463,187 (21.6)
H-2-----	{ 1274,640 (18.9)	² 594,526 (20.7)	² 478,969 (11.6)	117,432 (2.9)	56,745 (1.7)	93,116 (3.6)	118,287 (6.2)	55,606 (3.9)	20,813 (2.0)	41,363 (7.4)	42,285 (16.5)	172,162 (8.0)
Northern Lake Huron (H-1 and H-2)-----	{ 650,217 (44.7)	1,349,888 (46.9)	1,466,435 (35.4)	741,102 (18.3)	422,428 (12.7)	471,221 (18.3)	491,161 (25.9)	596,998 (41.4)	394,568 (38.7)	221,490 (39.7)	183,336 (71.8)	635,349 (29.6)
H-3-----	{ 98,818 (6.8)	¹ 247,572 (8.6)	² 470,423 (11.4)	137,463 (3.4)	14,130 (0.4)	14,399 (0.6)	8,907 (0.5)	8,006 (0.6)	2,798 (0.3)	9,163 (1.7)	557 (0.2)	92,021 (4.3)
H-4-----	{ 571,605 (39.2)	¹ 1,043,395 (36.2)	¹ 948,085 (47.0)	² 2,462,958 (60.8)	761,562 (22.8)	194,945 (7.6)	212,513 (11.2)	128,717 (8.9)	155,091 (15.2)	55,885 (10.0)	25,945 (10.2)	687,337 (32.0)
Central Lake Huron (H-3 and H-4)-----	{ 670,423 (46.0)	1,290,967 (44.8)	2,418,508 (58.4)	2,600,421 (64.2)	775,692 (23.2)	209,344 (8.2)	221,420 (11.7)	136,723 (9.5)	157,889 (15.5)	65,048 (11.7)	26,502 (10.4)	779,358 (36.3)
H-5-----	{ 62,987 (4.3)	91,493 (3.2)	74,038 (1.8)	¹ 513,409 (12.7)	² 1,676,432 (50.3)	784,215 (30.5)	273,421 (14.4)	119,140 (8.3)	66,825 (6.6)	41,915 (7.5)	12,247 (4.8)	337,830 (15.8)
H-6-----	{ 72,741 (5.0)	147,092 (5.1)	180,791 (4.4)	195,402 (4.8)	¹ 459,349 (13.8)	² 1,103,453 (43.0)	² 908,805 (48.0)	589,308 (40.8)	399,399 (39.2)	229,516 (41.1)	33,098 (13.0)	392,632 (18.3)
Southern Lake Huron (H-5 and H-6)-----	{ 135,728 (9.3)	238,585 (8.3)	254,829 (6.2)	708,811 (17.5)	2,135,781 (64.1)	1,887,668 (73.5)	1,192,226 (62.4)	708,448 (49.1)	466,224 (45.8)	271,431 (48.6)	45,345 (17.8)	730,462 (34.1)
Lake Huron (all 6 districts)-----	1,456,368	2,879,440	4,139,772	4,050,334	3,333,901	2,568,233	1,894,807	1,442,169	1,018,681	557,969	255,183	2,145,169
Percentage of average-----	68	134	193	189	155	120	88	67	48	26	12	-----

¹ Year of introduction of deep trap net.² Years of heaviest production of whitefish in deep trap nets.

all-time high in 1931 without the benefit of a really significant contribution from the southern region of the lake (H-5 and H-6) where the increase from 1929 to 1931 amounted to only 119,000 pounds.

In 1932 the first three districts, H-1, H-2, and H-3, after 2 peak years, suffered a severe decline in production. The combined decrease amounted to more than a million pounds. This reduction was compensated to a large extent by further increases in H-4, the center of the deep-trap-net fishery in 1932, and by the phenomenal rise in output in H-5, into which district deep trap nets were introduced for the first time. As a result, the total catch for the lake fell only slightly from the 1931 maximum.

After 2 years of extremely high production the catch of whitefish in H-4 decreased 1,701,000 pounds in 1933. The yield in the first four districts combined dropped from 3,342,000 pounds in 1932 to 1,198,000 pounds in 1933, a decrease of 2,144,000 pounds. It was hardly to be expected that this large decline in the first four districts could be compensated fully by a rise in production in southern Lake Huron, a region that produced only 136,000 pounds of whitefish in 1929. The increase in catch in southern Lake Huron was nevertheless enormous—1,163,000 pounds in H-5, 264,000 pounds in H-6, and 1,427,000 pounds in the two districts combined. In H-5 the 1933 production was 26.6 times the yield in 1929; for H-5 and H-6 combined the 1933 catch was 15.7 times that of 1929. The production in the entire lake, however, decreased in 1933 by 716,000 pounds.

The output of whitefish increased markedly in H-6 in 1934 (increase of 644,000 pounds), but the larger decrease of 892,000 pounds in H-5 led to a drop of 248,000 pounds in southern Lake Huron. Increases ranging from an insignificant recovery in H-3 to a sharp rise in H-2 occurred in the first three districts. In H-4, however, the catch dropped 567,000 pounds (from 762,000 pounds in 1933 to 195,000 pounds in 1934). The decrease for all six districts was 766,000 pounds.

The increases in the catch of whitefish in H-2 and H-4 in 1935 exceeded the decreases in H-1 and H-3; consequently, the totals increased slightly in both northern and central Lake Huron. However, the large decreases in H-5 and H-6 (705,000 pounds for the two districts) caused the yield of the entire lake to decline 673,000 pounds.

With the onset of the decline in production in H-6 in 1935 the cycle of exploitation of the stocks of Lake Huron whitefish by means of the deep trap net was approaching its final stages. As the fishery failed in other areas deep-trap-net fishermen had moved on to new grounds. H-6, however, had provided the last unexploited fishing area available. The lack of new grounds may account for the fact that large numbers of deep-trap-net fishermen remained longer in H-6 than they had in any other district. H-6, despite a continued decline in the catch, maintained first rank among the districts in the production of whitefish during the 5-year period, 1934-1938, relinquishing this position only with the almost complete collapse of the fishery in 1939.

It is true that in some districts the general decline during the later years of the fishery was interrupted by temporary increases as fishermen returned to glean a scant harvest from their former grounds. The most noteworthy recovery occurred in H-1, where in 1936 the production of whitefish rose above a half million pounds. However, the deep-trap-net operations in H-1 in 1936 were not centered in the southeastern part of the district (especially in Hammond Bay) as in earlier years but were carried on chiefly in the northwestern end (Cheboygan-St. Ignace) in an area that formerly had been exploited only moderately. These temporary increases in certain districts were insufficient by far to halt the general downward trend of the catch in the lake as a whole.

An outstanding feature of the statistical data discussed in the preceding pages was the shift from year to year in the center of production of whitefish. The output fluctuated over a wide range in all districts. Especially striking, however, were the increases in southern Lake Huron which accounted for only 9.3 percent of the 1929 production but yielded more than 60 percent of the total for the lake in 1933, 1934, and 1935 (73.5 percent in 1934).

These violent fluctuations in production and shifts in the center of operations suggest distinctly abnormal conditions in the fishery. The belief that conditions were abnormal in the years following 1929 finds support in the data on the catch of whitefish in the various districts in the earlier period of the fishery, 1891-1908 (table 6). Although a certain amount of shifting did occur in the relative importance of the several districts for the production of whitefish, these changes were insignificant in comparison with the tremendous fluctuations that took place during the recent years, 1930-1939 (table 5). In the earlier period, for example, H-1 and H-4 held first or second rank in every year except 1891 when the second highest yield was made in H-2 (H-1 in first position and H-4 in the third). Third and fourth rankings usually were held by H-2 and H-3 (characteristically in that order) while H-6 commonly ranked fifth and H-5 was normally sixth (only one exception). The limited extent of the fluctuations in the rankings of the districts with respect to the production of whitefish in 1891-1908 is brought out by the following tabulation (left half) which shows the number of years each position was held by each district. The right half of the tabulation brings out the sharp contrast in yield with that for the period of the deep-trap-net fishery, 1930-1939:

District	Rank (1891-1908)						District	Rank (1930-1939)					
	1	2	3	4	5	6		1	2	3	4	5	6
H-1-----	12	6	--	--	--	--	H-1-----	1	7	1	1	--	--
H-2-----	--	1	12	3	2	--	H-2-----	--	1	2	--	6	1
H-3-----	--	--	4	12	2	--	H-3-----	--	--	--	2	1	7
H-4-----	6	11	1	--	--	--	H-4-----	3	1	3	3	--	--
H-5-----	--	--	--	--	1	17	H-5-----	1	1	2	3	1	2
H-6-----	--	--	1	3	13	1	H-6-----	5	--	2	1	2	--

The range of rank was the greater in the more recent period in each district except H-3, a region in which the whitefish fishery was unimportant after 1932. The greatest increase in range occurred in H-5 which held every position from first to sixth although this area had ranked sixth 17 times (fifth in the remaining year) in the period, 1891-1908, and had not yielded more than 7,500 pounds in any one of the 18 years.

It should be noted further that with only one exception (the rank of 5) each of the rankings from 1 to 6 occurred in more districts in 1930-1939 than in 1891-1908. For example, first position was held in four districts (all but H-2 and H-3) in the more recent period as compared with only two (H-1 and H-4) in the earlier years, second rank was held by four districts in 1930-1939 as compared with three in 1891-1908,***.

The actual figures of catch of tables 5 and 6 support the observations based on the rankings, for the yields of the individual districts were in general far less variable in the early than in the recent period.

TABLE 6.—*Production of whitefish in pounds in Lake Huron according to statistical districts, 1891-1908*

Year	Statistical district						Total
	H-1	H-2	H-3	H-4	H-5	H-6	
1891	1,304,220	133,000	58,500	91,540	6,000	31,600	1,624,860
1892	1,150,933	94,000	29,200	160,450	3,500	48,100	1,486,183
1893	1,204,400	12,000	131,500	199,900	2,000	27,800	1,577,600
1894	939,250	91,600	61,500	116,550	1,000	8,350	1,218,250
1895	614,830	75,550	39,500	203,687	1,500	10,800	945,867
1896	440,600	118,616	167,300	264,119	500	14,600	1,005,735
1897	392,100	141,555	38,300	285,200	4,000	4,805	865,960
1898	239,800	59,500	38,500	249,050	1,500	4,400	592,750
1899	201,600	96,000	36,100	306,560	1,800	3,520	645,580
1900	152,400	104,000	99,500	191,520	4,500	3,500	555,420
1901	219,025	137,000	154,300	263,720	5,000	9,200	788,245
1902	307,000	137,500	122,000	331,930	600	14,500	913,530
1903	312,700	106,100	70,700	436,360	400	11,200	937,460
1904	328,000	54,000	85,000	303,860	1,000	15,500	787,360
1905	381,200	30,300	29,800	208,260	3,500	21,800	674,860
1906	492,300	38,500	25,600	198,220	5,000	32,100	791,720
1907	658,500	45,000	64,600	282,772	3,300	78,800	1,132,972
1908	578,915	48,963	41,666	270,832	7,500	26,029	973,905
Average	550,987	84,621	71,865	242,474	2,922	20,367	973,236
Percentage	56.6	8.7	7.4	24.9	0.3	2.1	

The records of yield for the years, 1891-1908, indicate also that the percentages of the total catch of whitefish in the different districts were approximately normal in 1929, the only recent year (with data for each district separately) in which the statistics were not seriously distorted by the deep-trap-net fishery. It is true, the percentage distribution of the catch of whitefish in Lake Huron in 1929 (table 5) differed somewhat from that for the average for 1891-1908. It will be noticed, for example, that in 1929 the greatest production (39.2 percent) was from H-4 with H-1 in second position (25.8 percent) whereas in 1891-1908 the greatest average yield came from H-1 (56.6 percent) with H-4 in second position (24.9 percent). Among the remaining districts the percentages were higher in 1929 in H-2 (in part because of the catch in deep trap nets), H-5, and H-6, and possibly lower in H-3,²³ but the rankings of the districts were the same.

The differences in the values of these percentages are not large enough, however, to warrant the conclusion that the relative capacities of the various districts for the production of whitefish in 1929 were changed greatly from those of 1891-1908. Although the high percentage of the total yield of whitefish in H-4 in 1929 is in disagreement

²³ The division of the statistics for the earlier years was based on the location of the home port and not necessarily on the grounds actually fished. It is known that, in more recent years at least, some fishermen from Au Sable-Oscoda (H-3) have operated with gill nets in H-4 on the "Middle Grounds" off Saginaw Bay. In 1929 and 1930 these fishermen accounted for about 14 percent of the total whitefish catch of H-4. If this same percentage held for the earlier years the average production in H-3 and H-4 should have been 32,392 pounds and 281,947 pounds, respectively, instead of 71,865 pounds and 242,474 pounds as recorded in table 6; the percentages should have been 3.3 and 29.0 instead of 7.4 and 24.9. There is no reason to believe that the data for other districts were affected significantly by the division of the catch according to port.

with average conditions in 1891–1908, evidence that the 1929 percentage for the district did not represent an abnormal condition may be seen in the fact that the catch in H-4 exceeded that in H-1 in 6 successive years (1898–1903) of the 18 in the early period. The percentage of the Lake Huron catch produced in H-4 in 1929 apparently was somewhat above the average for the modern as well as the early period, as in the 9 years, 1920–1928, the percentage of whitefish taken in Saginaw Bay (in H-4) did not exceed 31.3 percent and averaged only 23.5 percent. (This statement is based on statistics published for Saginaw Bay and Huron proper by the Michigan Department of Conservation.)

The evidence, that the percentages of the 1929 yield of whitefish taken in the several districts were within the normal range of variation lends further support to the belief that the deep-trap-net fishery brought about abnormal conditions in 1930–1939.

CHANGES IN PRODUCTION IN LAKE HURON AS RELATED TO
FLUCTUATIONS IN THE ABUNDANCE OF WHITEFISH
AND IN THE INTENSITY OF THE FISHERY

Up to this point the discussion has been concerned only with the fluctuations in the catch of whitefish, because it was believed that this, the more obvious phase of the fishery, should be outlined clearly before the changes in production were analyzed in relation to concurrent fluctuations in the abundance of whitefish and the intensity of the whitefish fishery. The fundamental problem in the analysis of the statistical data relative to the whitefish fishery of Lake Huron is the determination of the probable effects of deep-trap-net operations on the abundance of marketable whitefish. As pointed out previously (p. 315) this problem is complicated greatly by the circumstance that whitefish are known to have been abnormally abundant during the years in which the deep-trap-net fishery was undergoing its most rapid expansion. The abundance of whitefish in Lake Huron was possibly above normal in 1929; certainly it was well above normal in 1930 and 1931 (table 10). A decline from this abnormally high abundance would have occurred even if deep trap nets had not been operated in the lake. It is only logical to believe also that the high abundance following 1929 would have stimulated fishing intensity even had deep trap nets not been fished. The general problem resolves itself, therefore, into the estimation of the degree to which the increased fishing intensity and the heightened production made possible by the use of deep trap nets affected the rate of the decline in abundance and its ultimate extent.

That the deep trap net accounted for the bulk of the extremely high yields of whitefish over the period, 1930–1935, was brought out in the preceding section. It will now be demonstrated that the high production resulted from an unreasonably great fishing intensity and that this overfishing in turn accelerated the decline in the abundance of whitefish. In the four southernmost districts in which the deep trap net was fished most extensively the whitefish fishery reached a state of collapse. Abundance and catch were reduced in the other two districts in which the deep-trap-net operations were less extensive but the decline was far less pronounced than in the four districts.

A comparison of the extent of the changes in production, abundance, and fishing intensity in the several districts may be found in table 7. In this one table the year 1929 rather than the 11-year period (1929–1939) has been taken as the point of reference. To be sure, there is no certainty that 1929 was a "normal" year. However, the catch in 1929 was at approximately the typical level for 1922–1929, and there is no evidence of any unusual conditions in the fishery in that year. Certainly, 1929 is the most nearly normal year for which detailed statistical data are available.

The data of table 7 do not provide a complete history of the deep-trap-net fishery. They do serve, however, to show the variation among the districts in the maxima of yields and fishing intensity that followed the introduction of the deep trap net, and the apparent relationship between these maxima and conditions in 1939. The increases in catch were by no means as great in H-1 and H-2 as in the remaining districts. In

these two northern districts the maximum productions were 263 and 317 percent, respectively, of the 1929 yield. In central Lake Huron the maxima were 476 percent in H-3 and 431 percent in H-4. It was in southern Lake Huron, however, that the greatest relative increases in production occurred. The maximum yield was more than 26 times the 1929 catch in H-5 and more than 15 times the 1929 production in H-6.

The differences in the relative maximum yields attained in the several districts are to be attributed primarily to differences in the relative increases in fishing intensity. The maximum intensity in H-1 and H-2 was a little more than twice that of 1929. It was roughly 5 times the 1929 level of intensity in H-3 and 4 times in H-4. In H-5 and H-6, however, the maximum fishing intensities were, respectively, 42 and 27 times the 1929 intensity.

The relative maximum abundance attained in the various districts exhibited remarkable agreement. In four of the six districts (H-1, H-4, H-5, and H-6) the maximum abundance was between 140 and 150 percent of the abundance in 1929, and in a fifth (H-2) the maximum was a little less than 140 percent (136 percent) of the 1929 level. In H-3 the greatest estimated abundance occurred in 1929 in which year the pound nets were particularly successful (table 11). The abundance in H-3 fell in 1930 but increased in 1931; peculiarly enough the abundance in 1931 was 143 percent of that in 1930 (*cf.* increases in other districts over 1929 abundance).

Production and abundance in 1939 were below the 1929 level in every district, and the fishing intensity was less than that of 1929 in all but the two southernmost districts. Of especial significance is the fact that the abundance in 1939 was relatively much higher in H-1 and H-2, the two districts in which production and intensity had reached the relatively lowest maxima. In the remainder of the lake the whitefish had almost disappeared. So great was the depletion that in H-5 and H-6

TABLE 7.—Maximum and 1939 production and abundance of whitefish and maximum and 1939 fishing intensity for whitefish expressed as percentages of the 1929 values in each statistical district of Lake Huron

District	Year of maximum production	Production		Year of maximum intensity	Intensity		Year of maximum abundance	Abundance	
		Maximum	1939		Maximum	1939		Maximum	1939
H-1.....	1931	263	38	1931	233	89	1930	140	41
H-2.....	1930	317	23	1930	228	50	1930	136	43
H-3.....	1931	476	1	1931	528	5	1929	100	6
H-4.....	1932	431	5	1932	377	60	1931	149	7
H-5.....	1933	2,662	19	1933	4,211	433	1931	142	5
H-6.....	1934	1,517	46	1935	2,678	489	1932	148	10

¹ The deep-trap-net fishery of 1929 was excluded in the computations of these percentages of production and fishing intensity for H-2.

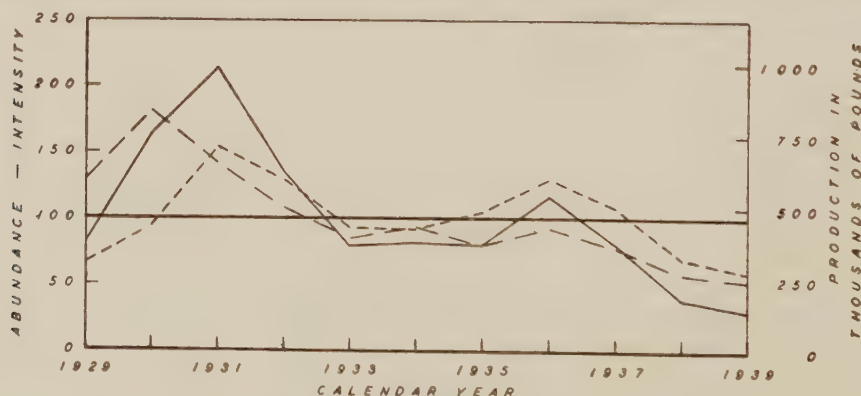


FIGURE 5.—First district, H-1.

Figures 5 to 10 show the annual fluctuations in the production (solid lines) and abundance (long dashes) of whitefish and in the intensity of the whitefish fishery (short dashes) over the period, 1929-1939, in each of the six statistical districts of Lake Huron (see fig. 4). In each figure the central horizontal line represents the average conditions for the 11 years, 1929-1939.

fishing intensities between 4 and 5 times those of 1929 yielded productions amounting to only 19 and 46 percent, respectively, of the 1929 catch. For practical purposes it can be said that there was no whitefish fishery in H-3 in 1939, and that the fishery in H-4 was insignificant.

The data of table 7 have brought out the fact that a disastrous depletion of the

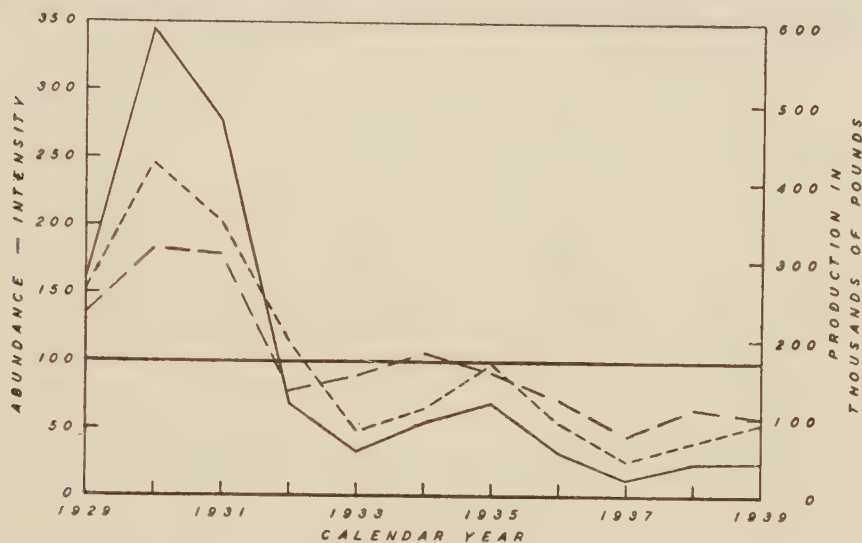


FIGURE 6.—Second district, H-2.

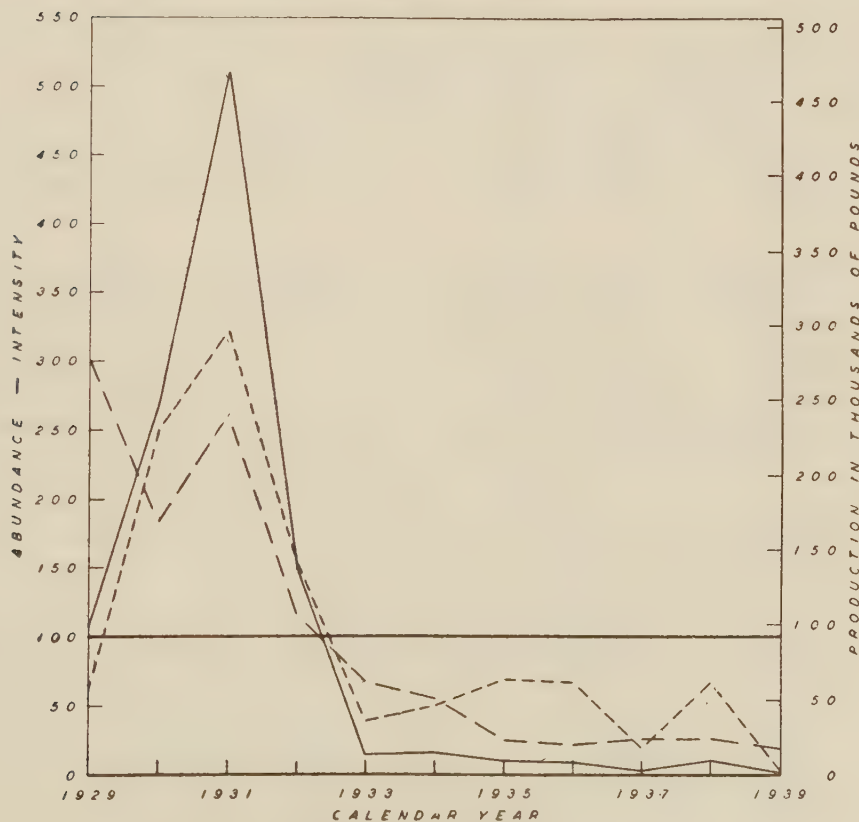


FIGURE 7.—Third district, H-3.

whitefish occurred in the four districts in which the use of the deep trap net led to an excessive multiplication of fishing intensity and catch. The decline in the abundance of whitefish was much less severe in the two districts in which the exploitation of the stock was more moderate. Further evidence on the harmful effects of deep-trap-net operations will be brought out by a more detailed consideration of the annual changes in production, fishing intensity, and abundance in the various districts with reference to the 1929–1939 averages.

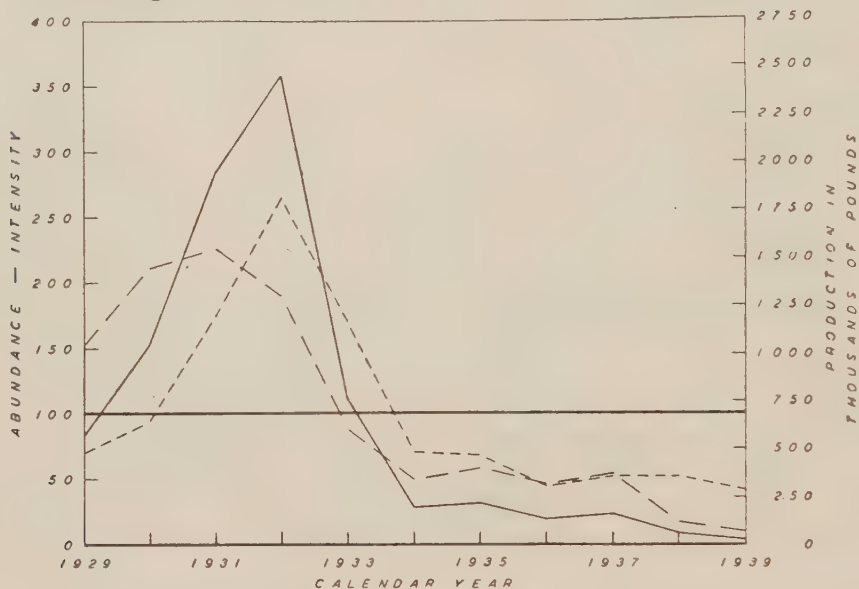


FIGURE 8.—Fourth district, H-4.

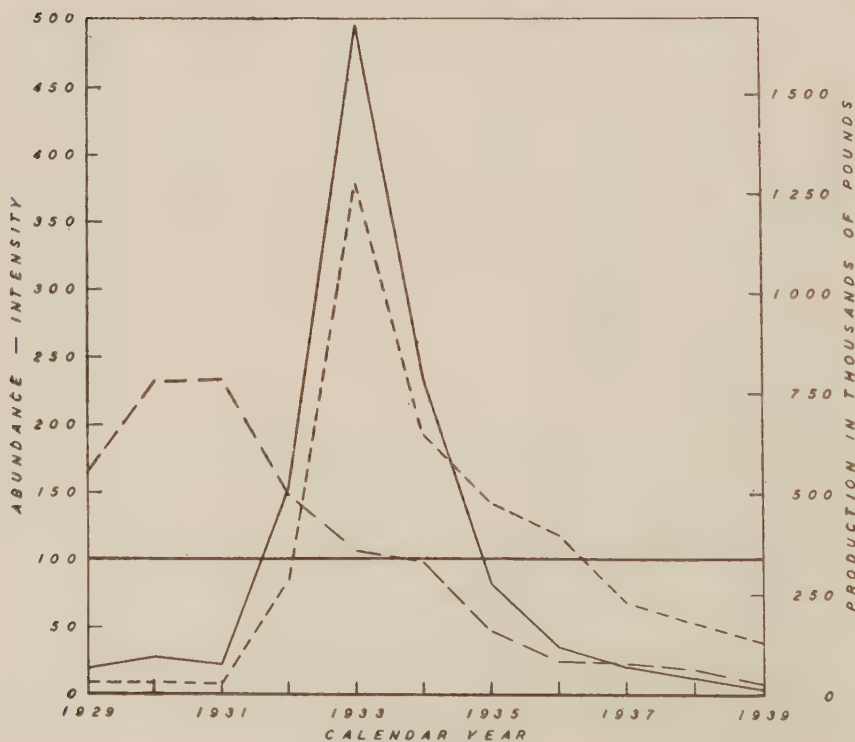


FIGURE 9.—Fifth district, H-5.

In the previous section attention was called to the existence of a typical deep-trap-net cycle of production (p. 319) in which the catch "was raised to tremendous heights for about 2 years, only to fall away sharply." It is equally valid to speak of "typical deep-trap-net cycles" of fishing intensity and in the abundance of whitefish. (For graphical representations of the annual fluctuations in the catch and abundance of whitefish and in the intensity of the whitefish fishery in the several districts, see figs. 5 to 10.) The tremendous increases in yields were accompanied by

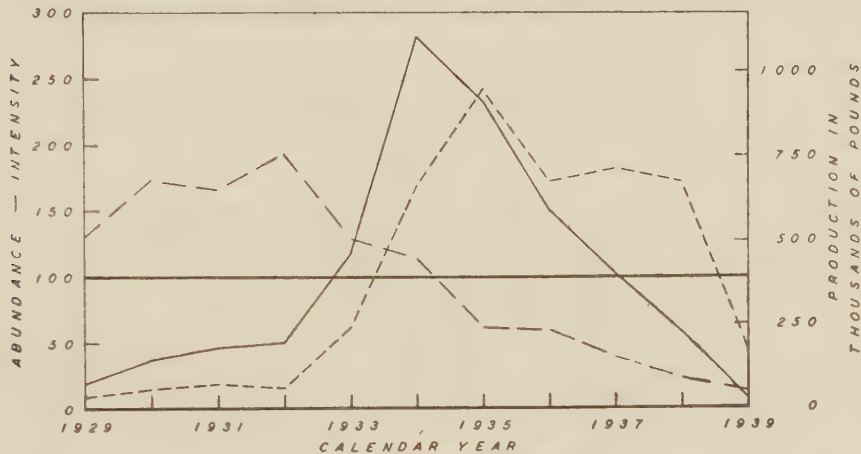


FIGURE 10.—Sixth district, H-6.

great increases in fishing intensity (table 8). To a large extent these increases in intensity represented deep-trap-net operations (table 9). In about 2 years, however, the fishing intensity declined in a district as the fishermen moved on to more productive grounds. An exception to this cycle of intensity is to be found in H-6 where an extremely intensive fishery was carried on for 5 years (1934–1938) despite a rapid decrease in the returns. Operators of deep trap nets remained longer in H-6 because the more northerly grounds had been exploited thoroughly in previous years (p. 321). H-1 and H-2 showed limited secondary increases in fishing intensity (about 1935–1937 in H-1 and 1934–1935 in H-2) as some fishermen returned from the depleted grounds in the south.

Without exception the abundance of whitefish fell sharply after a period (usually 2 years) of intensive deep-trap-net operations. This fact is brought out clearly by the data of table 10 in which the years of greatest production of deep trap nets have been designated. (The comparison of tables 4 and 9 will reveal that the years of greatest yields of deep trap nets and the years of greatest intensity of the deep-trap-net fishery were not always the same.) The nature of the changes in abundance that followed heavy removals of whitefish may be summarized for the districts as follows:

H-1. Abundance began to decline in 1931, the second year of heavy production by deep trap nets. This decline continued through 1933.

TABLE 8.—Annual fluctuations in the intensity of the fishery for whitefish in each district of Lake Huron

[Expressed as percentages of the average 1929–1939 intensity in the district]

District	Fishing intensity as percentage of average in year										
	1929	1930	1931	1932	1933	1934	1935	1936	1937	1938	1939
H-1.....	66	94	154	129	93	92	105	130	108	70	59
H-2.....	152	246	203	114	48	65	98	54	26	40	54
H-3.....	61	250	322	153	39	50	69	67	19	67	3
H-4.....	70	94	174	264	170	70	68	44	52	52	42
H-5.....	9	9	8	84	379	192	141	118	68	53	39
H-6.....	9	15	19	16	62	168	241	172	182	172	44

H-2. Abundance was high in 1930 and 1931, the years of high yields; in 1932 abundance declined to less than half that of 1931.

H-3. Abundance increased in 1931, the second year of heavy production, but was less than half as great in 1932 as in 1931.

H-4. Abundance decreased somewhat in 1932, the second year of high production; the abundance in 1933 was less than half that of 1932.

TABLE 9.—*Annual fluctuations in the intensity of the whitefish fishery for all six districts of Lake Huron combined (third row from bottom of table) and distribution of each year's fishing intensity among the districts*

[The average annual intensity for the entire lake, 1929-1939, is 100.0. In parentheses are the intensity values of the deep-trap-net fishery. The value of one unit is 1/1,100 of the total expected catch (p. 314) of all districts, 1929-1939]

District or area	Fishing intensity in year											Total	Percentage of intensity represented by deep trap nets
	1929	1930	1931	1932	1933	1934	1935	1936	1937	1938	1939		
H-1.....	{ 13.8 (7.5)	{ 19.9 (7.5)	{ 32.4 (13.0)	{ 27.0 (8.1)	{ 19.6 (4.5)	{ 19.3 (4.2)	{ 22.0 (7.3)	{ 27.3 (16.0)	{ 22.7 (13.5)	{ 14.7 (7.4)	{ 12.6 (6.2)	{ 231.3 (87.7)	{ 37.9
H-2.....	{ 9.7 (2.8)	{ 15.5 (9.5)	{ 12.8 (10.1)	{ 7.2 (5.7)	{ 3.1 (1.5)	{ 4.1 (2.2)	{ 6.2 (4.7)	{ 3.4 (3.1)	{ 1.7 (1.3)	{ 2.5 (2.4)	{ 3.4 (3.4)	{ 69.6 (46.7)	{ 67.1
Northern Lake Huron (H-1 and H-2).....	{ 23.5 (2.8)	{ 35.4 (17.0)	{ 45.2 (23.1)	{ 34.2 (13.8)	{ 22.7 (6.0)	{ 23.4 (6.4)	{ 28.2 (12.0)	{ 30.7 (19.1)	{ 24.4 (14.8)	{ 17.2 (9.8)	{ 16.0 (9.6)	{ 300.9 (134.4)	{ 44.7
H-3.....	{ 1.6 (4.6)	{ 6.3 (4.6)	{ 8.2 (7.0)	{ 3.9 (3.5)	{ 1.0 (0.7)	{ 1.2 (1.0)	{ 1.7 (1.6)	{ 1.7 (1.6)	{ 0.5 (0.4)	{ 1.7 (1.6)	{ 0.1 (0.1)	{ 27.9 (22.1)	{ 79.2
H-4.....	{ 16.4 (4.5)	{ 21.8 (4.5)	{ 40.2 (16.6)	{ 61.2 (47.4)	{ 39.4 (30.8)	{ 16.2 (11.2)	{ 15.6 (10.7)	{ 10.1 (7.2)	{ 12.0 (9.2)	{ 12.1 (10.7)	{ 9.7 (8.6)	{ 254.7 (156.9)	{ 61.6
Central Lake Huron (H-3 and H-4).....	{ 18.0 (9.1)	{ 28.1 (9.1)	{ 48.4 (23.6)	{ 65.1 (50.9)	{ 40.4 (31.5)	{ 17.4 (12.2)	{ 17.3 (12.3)	{ 11.8 (8.8)	{ 12.5 (9.6)	{ 13.8 (12.3)	{ 9.8 (8.7)	{ 282.6 (179.0)	{ 63.3
H-5.....	{ 1.8 (15.7)	{ 1.9 (15.7)	{ 1.5 (15.7)	{ 16.6 (74.5)	{ 75.3 (38.1)	{ 38.2 (27.7)	{ 27.9 (23.4)	{ 23.4 (13.5)	{ 13.6 (10.5)	{ 10.6 (7.7)	{ 7.7 (7.7)	{ 218.5 (211.1)	{ 96.6
H-6.....	{ 2.5 (12.6)	{ 4.0 (42.2)	{ 5.1 (62.9)	{ 4.4 (45.5)	{ 16.9 (45.5)	{ 45.4 (45.5)	{ 65.3 (45.5)	{ 46.5 (45.5)	{ 49.2 (48.5)	{ 46.6 (46.4)	{ 12.1 (12.0)	{ 298.0 (270.1)	{ 90.6
Southern Lake Huron (H-5 and H-6).....	{ 4.3 (15.7)	{ 5.9 (87.1)	{ 6.6 (87.1)	{ 21.0 (87.1)	{ 92.2 (80.3)	{ 83.6 (80.3)	{ 93.2 (90.6)	{ 69.9 (68.9)	{ 62.8 (62.0)	{ 57.2 (56.9)	{ 19.8 (19.7)	{ 516.5 (481.2)	{ 93.2
Lake Huron (all 6 districts).....	{ 45.8 (2.8)	{ 69.4 (26.1)	{ 100.2 (46.7)	{ 120.3 (80.4)	{ 155.3 (124.6)	{ 124.4 (98.9)	{ 138.7 (114.9)	{ 112.4 (96.8)	{ 99.7 (86.4)	{ 88.2 (79.0)	{ 45.6 (38.0)	{ 1,100.0 (794.6)	{ 72.2
Percentage of intensity represented by deep trap nets.....	6.2	37.6	46.6	66.8	80.2	79.5	82.8	86.1	86.7	89.6	83.3	72.2	-----

¹ Value too low; the estimate of the total intensity for H-4 in 1931 and 1932 included consideration of large catches for which gear records were lacking, but a large part of which was taken by deep trap nets. Other totals and percentages in the computation of which these figures were involved were affected, but relatively less severely than those indicated by the footnote.

H-5. Abundance decreased considerably in 1933, the first of the two years of heaviest production, and declined slightly in 1934, the second of these years. In 1935 after the two years of heaviest production the abundance fell to less than half the 1934 level.²⁴

H-6. Abundance declined somewhat in 1934, the first year of heaviest production, and fell sharply in 1935, the second year. (See footnote 24.) The decline was small in 1936 but a rapid rate of decrease was resumed in 1937.

Comment was omitted deliberately on the recorded decreases in abundance from 1931 to 1932 in H-5 and from 1932 to 1933 in H-6. Because of the difficulty of bridging the gap between a fishery dominated by gill nets and pound nets to one dominated by deep trap nets (p. 316) there is some question as to the accuracy of the comparison between the two years involved in each district. However, comparisons are valid within each of the periods, 1929-1931 and 1932-1939 in H-5, and 1929-1932 and 1933-1939 in H-6. Consequently the observations on the change in abundance that followed the extensive use of deep trap nets in these two districts also are valid. Furthermore,

²⁴ Part of the decline from 1933 to 1934 and 1934 to 1935 may be attributed to the fact that effective August 1, 1934, deep trap nets were restricted in Lake Huron to water with depths of 80 feet or less.

TABLE 10.—*Annual fluctuations in the abundance percentages for whitefish in the various districts and areas of Lake Huron, 1929-1939*

[Expressed as percentages of average 1929-1939 abundance. In the computation of percentages for areas of more than one district and for the entire lake, the abundance percentage for each district was weighted according to the percentage of the total 1929 production contributed by that district]

District or area	Abundance percentage in year										
	1929	1930	1931	1932	1933	1934	1935	1936	1937	1938	1939
H-1.....	129	¹ 181	¹ 141	108	85	94	80	93	78	58	53
H-2.....	¹ 135	¹ 183	¹ 179	78	89	106	91	71	45	65	58
Northern Lake Huron (H-1 and H-2)...	131	182	157	95	87	99	85	84	64	61	55
H-3.....	301	¹ 183	² 261	115	67	55	25	22	26	26	19
H-4.....	152	¹ 211	² 226	¹ 189	88	49	58	46	54	17	10
Central Lake Huron (H-3 and H-4)...	174	207	231	178	85	50	53	43	50	18	11
H-5.....	164	231	233	¹ 147	² 106	98	47	24	23	19	8
H-6.....	130	173	166	193	¹ 129	² 114	² 61	59	39	23	13
Southern Lake Huron (H-5 and H-6)...	146	200	197	172	117	107	54	43	32	21	11
Lake Huron (all 6 districts).....	152	195	195	140	89	77	67	61	55	38	31

¹ Year of introduction of the deep trap net.

² Years of greatest production by deep trap nets.

TABLE 11.—*Annual fluctuation in the catch of whitefish per unit of fishing effort of gill nets, deep trap nets, and pound nets in the various districts of Lake Huron, 1929-1939*

District	1929	1930	1931	1932	1933	1934	1935	1936	1937	1938	1939	Average
Pounds of whitefish per 10,000-foot-lift of gill nets												
H-1.....	109.4	115.9	99.4	65.3	67.8	70.2	56.8	57.8	56.7	91.1	44.1	75.9
H-2.....	29.4	61.8	48.8	10.8	16.6	21.8	15.0	15.3	6.1	-----	2.0	22.8
H-3.....	62.5	60.6	48.7	24.7	16.7	11.5	8.4	6.1	9.0	3.8	4.6	33.3
H-4.....	72.1	81.5	69.3	63.7	13.7	40.5	4.1	-----	5.6	4.2	6.4	36.1
H-5.....	131.2	187.5	186.0	137.4	87.3	14.1	6.4	-----	8.7	3.4	-----	84.7
H-6.....	88.8	115.8	107.9	134.4	106.6	83.0	33.6	18.5	24.0	14.2	-----	72.7
Pounds of whitefish per lift of one deep trap net												
H-1.....	-----	167.7	125.6	91.7	61.8	108.5	97.3	94.5	76.2	43.3	51.3	91.8
H-2.....	115.2	141.9	139.1	62.2	73.0	76.3	75.8	56.6	40.4	52.8	45.7	79.9
H-3.....	-----	282.4	476.1	206.1	115.3	99.1	41.5	39.2	41.7	45.9	-----	149.7
H-4.....	-----	127.3	470.4	340.7	168.3	87.5	108.2	87.1	110.8	30.0	18.2	154.9
H-5.....	-----	-----	-----	404.3	295.9	272.9	130.8	67.5	65.2	52.8	21.3	163.8
H-6.....	-----	-----	-----	-----	402.5	372.3	202.2	197.2	127.3	76.8	41.9	202.9
Pounds of whitefish per lift of one pound net												
H-1.....	65.2	120.5	93.7	78.4	54.6	50.7	35.8	47.1	42.8	29.2	24.2	58.4
H-2.....	70.2	94.6	97.1	43.1	49.1	65.8	39.6	34.1	-----	5.2	-----	55.4
H-3.....	98.3	68.5	53.1	12.2	-----	-----	4.5	-----	-----	3.2	-----	47.3
H-4.....	33.1	57.5	40.0	35.1	13.8	9.8	11.3	8.1	5.0	4.5	2.5	20.1
H-5.....	46.1	60.2	78.5	100.3	26.2	12.3	101.2	3.1	-----	-----	-----	53.5
H-6.....	30.0	42.0	51.7	38.8	25.1	18.7	9.9	11.7	5.3	12.3	6.6	22.9

these same decreases are apparent in the records of the actual catch per lift of deep trap nets in these same districts (table 11).

The history of the annual fluctuations in the abundance of whitefish in the years subsequent to the decline that followed immediately upon the extensive use of the deep trap net varied widely among the districts.

In H-1, where the use of deep trap nets may be described as "moderate," the abundance percentage for whitefish dropped to 85 in 1933, fluctuated irregularly in 1933-1937, and declined to a level of less than 60 percent in 1938 and 1939. Abundance did not fall significantly below 80 before 1938. In H-2, the other district in which the maxima of production and fishing intensity were relatively low, the sudden decline to

78 percent in 1932 was followed by recoveries in 1933 and 1934 (89 and 106 percent, respectively) and relatively high abundance in 1935 (91 percent). The decreases in 1935-1937 that led to the minimum of 45 in 1937 were followed by a recovery in 1938 and a slight decline in 1939. In both H-1 and H-2 the secondary declines in abundance were preceded by secondary increases in fishing intensity—increases traceable to revivals of deep-trap-net operations.

The remaining districts experienced greater ultimate declines than did H-1 and H-2. Furthermore, these districts failed to show recoveries comparable to those that occurred in H-1 and H-2. In H-3 the decline in abundance continued through 1935; abundance remained rather stable at about 25 in the years, 1935-1938, and declined to 19 in 1939. The abundance in H-4 declined through 1934, was at approximately 50 percent in 1934-1937, and dropped to an extremely low level in 1938 and 1939. In both H-5 and H-6 the decline in abundance that followed the introduction of the deep trap net proceeded without interruption (albeit at an irregular rate) through 1939. In that year whitefish were extremely scarce in both districts.

The data that have been discussed in the preceding pages support the general conclusion that the deep trap net was in large measure responsible for a disastrous depletion of the whitefish in the four southernmost districts of Lake Huron. This depletion was the result of the unreasonable increases in fishing intensity and hence in production in these districts. In the northern portion of the lake where the net was used more moderately the decline in the abundance of whitefish was severe but it did not reach such extremes as were found in the central and southern regions of the lake.

Largely for the sake of completeness the annual fluctuations of production, abundance, and fishing intensity for all six districts combined have been presented graphically in figure 11 (data from tables 5, 9, and 10). To some extent the data for the entire

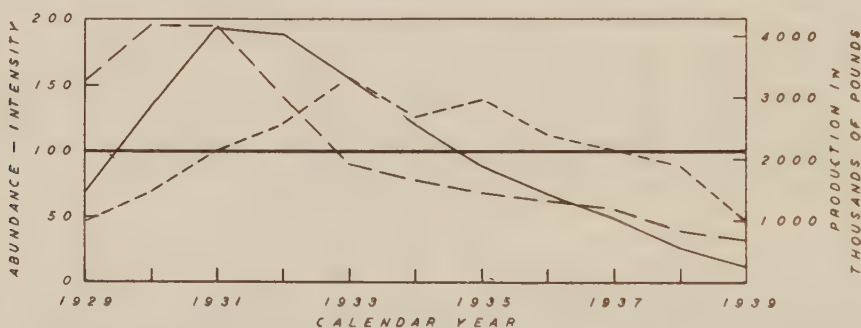


FIGURE 11.—Annual fluctuations in the production (solid line) and abundance (long dashes) of whitefish and in the intensity of the whitefish fishery (short dashes) in Lake Huron (all six districts combined), 1929-1939.

lake lack significance as the combination of the data for all districts obscures the extreme nature of the fluctuations that took place within the individual districts. The data serve chiefly to show that a relatively great abundance of whitefish contributed materially to the high production in 1930-1932 (especially in 1930 and 1931), and that the decline in catch subsequent to 1932 would have been much more rapid had not the intensity of the fishery been so great. Although the decline in abundance began in 1932 the intensity of the fishery increased rapidly until 1933. Beyond 1932 the abundance of whitefish was below the 11-year average and decreasing in every year. Fishing intensity, however, did not return to the 11-year average before 1937 or to the 1929 level before 1939.

The question now arises, "What characteristics made the deep trap net so deadly effective?" The tremendous production of deep trap nets was possible chiefly because: (1) they can be set in deeper water, and hence in areas with greater concentrations of whitefish, than can the pound nets; and (2) they are much more efficient in taking whitefish than are gill nets fished on the same grounds. Attention will be given first to the advantages of the deep trap net over the pound net.

In size and construction the pound net and deep trap net resemble each other so closely that the latter gear was known in some localities as the "submarine pound net" (p. 300). If the two gears are fished in the same depth of water neither has an important advantage over the other.²⁵ However, pound nets which are held in place by stakes driven into the bottom of the lake, and have cribs or pots extending from the bottom to above the surface, ordinarily cannot be fished successfully at depths greater than 80 feet. Most pound nets are operated in much shallower water. Deep trap nets, on the other hand, have covered cribs and are held in position by means of lines attached to anchors and by buoys. Consequently, they can be employed at all depths frequented by whitefish. The use of stakes also limits pound nets to areas with a soft bottom into which stakes can be driven. Deep trap nets do not suffer from this limitation.

A further advantage of the deep trap net lies in its greater mobility. Pound nets are fished in the same locality throughout the season (and usually year after year) but deep trap nets can be moved much more easily and consequently can be fished in the exact locations at which whitefish are found to be concentrated.

The vertical distribution of the whitefish will be treated in part III. It may be stated at this time, however, that usually whitefish are readily available to pound nets

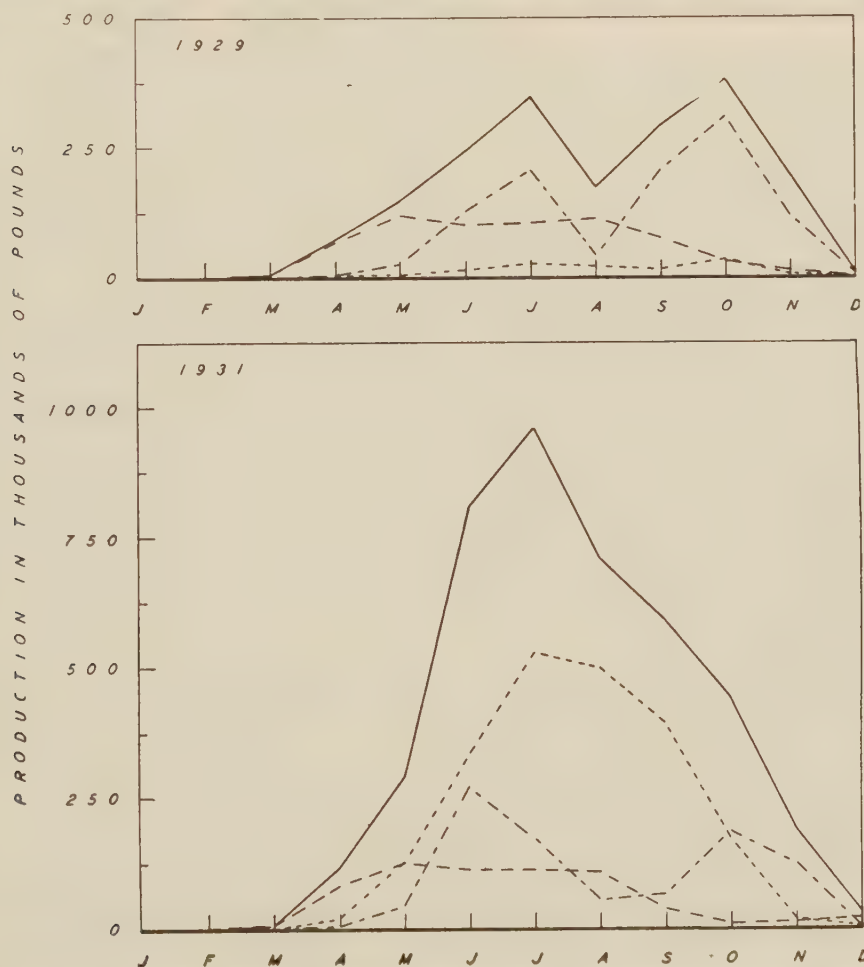


FIGURE 12.—Comparison of the monthly production of whitefish in the Michigan waters of Lake Huron in 1929 and 1931, to bring out the effects of the deep-trap-net fishery on the seasonal distribution of the catch. Gill nets, long dashes; deep trap nets, short dashes; pound nets, short and long dashes; total production, solid line.

²⁵ Field observations in northern Lake Michigan indicated that pound nets may take slightly more fish than deep trap nets fished at the same depth. This relationship is not surprising since the pound net is a "lighter" net (that is, the open top permits the free penetration of light) and would, therefore, be entered by fish more readily than the "darker" deep trap net. Also see table 51, appendix C.

TABLE 12.—*Monthly production of whitefish in Lake Huron, 1929 and 1931, in gill nets, deep trap nets, pound nets, and all gears combined*

[Percentages are in parentheses]

Gear	Production of whitefish in pounds in month												Total
	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
<i>1929</i>													
Gill net.....	180 (0.0)	580 (0.1)	2,465 (0.5)	52,029 (10.6)	94,066 (19.2)	79,724 (16.3)	82,332 (16.8)	88,890 (18.2)	58,534 (12.0)	21,744 (4.4)	8,848 (1.8)	569 (0.1)	489,961 (100.0)
Deep trap net.....				1,239 (1.4)	1,774 (2.0)	10,867 (22.5)	20,535 (23.6)	15,068 (17.3)	9,809 (11.3)	24,061 (27.6)	3,768 (4.3)		87,121 (100.0)
Pound net.....				1,278 (0.2)	19,582 (2.4)	101,424 (12.3)	165,066 (20.0)	33,145 (4.0)	163,763 (19.9)	244,055 (29.6)	91,878 (11.2)	2,505 (0.4)	823,696 (100.0)
All gears.....	180 (0.0)	580 (0.0)	2,468 (0.2)	57,764 (4.0)	117,463 (8.1)	193,906 (13.3)	276,917 (19.0)	137,161 (9.4)	233,074 (16.0)	302,087 (20.7)	130,694 (9.0)	4,074 (0.3)	1,456,368 (100.0)
<i>1931</i>													
Gill net.....	390 (0.1)	317 (0.1)	4,663 (0.7)	82,423 (13.3)	124,071 (20.0)	112,776 (18.2)	113,365 (18.3)	107,329 (17.3)	36,492 (5.9)	7,752 (1.2)	9,001 (1.5)	20,936 (3.4)	619,515 (100.0)
Deep trap net.....				19,220 (0.9)	115,241 (5.6)	334,943 (16.1)	528,609 (25.4)	498,984 (24.0)	391,921 (18.8)	172,701 (8.3)	15,757 (0.8)	2,220 (0.1)	2,079,596 (100.0)
Pound net.....		2 (0.0)	55 (0.0)	3,340 (0.4)	41,882 (4.6)	269,224 (29.5)	169,001 (18.5)	53,513 (5.9)	65,801 (20.3)	184,552 (13.4)	121,774 (13.4)	1,796 (0.2)	910,940 (100.0)
All gears.....	390 (0.0)	319 (0.0)	4,785 (0.1)	116,754 (2.8)	289,342 (7.0)	808,065 (19.5)	961,095 (23.2)	709,469 (17.2)	591,894 (14.3)	441,501 (10.7)	186,997 (4.5)	29,161 (0.7)	4,139,772 (100.0)

only during limited periods, one in late spring and early summer and another in mid-autumn. Many fishermen discontinue pound-net operations at other seasons. It is true also that even in periods of active operation the greatest concentrations of whitefish may be at depths beyond the reach of pound nets.

The offshore movement that leads to a concentration in relatively deep water in the summer and early autumn exposes the whitefish to the inroads of the deep trap net at the time it is most vulnerable. Formerly, the only toll on the whitefish in its summer concentration was that levied by gill nets, and in the modern fishery of Lake Huron this type of gear has not proved generally effective for the large-scale catching of whitefish. The gill net is so ineffective for the capture of whitefish under modern conditions that gill-net fisheries are supported by this species alone only in very limited areas or over extremely short periods of time (chiefly during the spawning season).²⁶ The large-mesh gill-net fishery is now conducted ordinarily for the capture of both trout and whitefish or of trout alone, but very seldom exclusively for the taking of whitefish.²⁷ The comparative ineffectiveness of gill nets made the time of summer concentration of the whitefish a "semi-closed" season during which the species was in large measure immune to capture. The introduction of the deep trap net made this same period the season of maximum production.

The effect of the deep-trap-net fishery on the monthly distribution of the whitefish catch and the high production this gear made possible in the summer months may be illustrated by the data of table 12 and figure 12. The gill-net season extended through the months, May-August, in both 1929 and 1931. (September was a fairly good month in 1929.) No distinct peaks occurred in either year. The pound-net catch, on the contrary, was divided into two distinct seasons, each with a sharp peak. The early-season maximum occurred in July in 1929 and in June in 1931. Both of the autumn maxima were in October. The 1931 data which show the more pronounced summer depression provide the better description of the monthly distribution of pound-net production because the 1929 early-summer peak was later and the September catch was relatively higher than usual. The data for both years, however, have a distinct late-summer minimum—August in 1929 and August-September in 1931.

The curve of total catch in 1929 has a minimum in August corresponding to the August depression in the pound-net data. A similar minimum would have existed in

²⁶ When gill nets were fished on the spawning grounds the catches were sometimes enormous—thousands of pounds in a single lift.

²⁷ This statement holds true even in Lake Michigan where the gill net is normally the dominant gear for the production of whitefish.

the curve of total production in 1931 if only gill nets and pound nets had been in operation. The deep-trap-net catch, however, changed the form of the curve completely. This gear not only deprived the whitefish of its former temporary respite during the period of habitation in deep waters, but actually exposed the fish to a far more severe exploitation in late summer than it had previously suffered at any season. From these facts it is obvious that effective regulation of the deep trap net must include the reduction of its catches on the deep-water grounds on which whitefish congregate during late summer.

The summer assemblings of whitefish that made possible the great effectiveness of the deep trap net seemingly were not as dense in northern Lake Huron as in the central and southern regions of the lake. In each of the four southerly districts the average catch per lift of deep trap nets exceeded 400 pounds in one year and was more than 200 pounds per lift in 2 or 3 years (table 11). In the northern districts the greatest average catch per lift of deep trap nets was 168 pounds in H-1 and 142 pounds per lift in H-2 (in 1930 in both districts). The relatively poor success of deep trap nets is the more remarkable in H-1 because that area under normal conditions had been an important and in many, if not the majority of years, the leading center of whitefish production in the lake. At any rate these small catches per lift account for the more moderate use of deep trap nets in H-1 and H-2.

A final point that deserves consideration is the possibility that mass migrations of whitefish may have played a role in the shift from year to year in the center of the deep-trap-net fishery. The failure of the grounds on which the deep trap nets first were fished and the resultant necessity for opening up new areas gave an early indication of the disastrous results to be expected from the unrestricted operation of this gear. Deep-trap-net fishermen denied most vigorously, however, that their activity had caused any depletion on the grounds. They contended that the fish had not been caught but that they merely had migrated to another area. They held further that in changing the center of the fishery they were only following the movements of the whitefish population. In support of their contention they stressed the argument that only mass migrations could make possible such high production in southern Lake Huron (H-5 and H-6), an area in which the catch of whitefish had always been small.

The assumption of a mass migration of whitefish proceeding in the same direction year after year runs counter to all known facts concerning the habits of the species. Nevertheless, the possibility cannot be denied that extraordinary conditions might bring about unusual reactions on the part of the fish. The strongest argument against the theory of mass migration lies in the fact that such an assumption is altogether unnecessary. The heavy yield in southern Lake Huron in 1932 and later years was not made possible, as fishermen contended, by the influx of whitefish from more northerly grounds. The records of the catch of gill nets per unit of effort (table 11) prove that dense concentrations of whitefish had been present on the offshore grounds of H-5 and H-6 for years before the deep trap net was introduced. In fact, the catch of whitefish per unit of effort of gill nets in H-5 exceeded that in every other district during the four years, 1929-1932. The catch per unit of effort of gill nets in H-6 was greater than that in any other district in 1933 and was second only to the catch per lift in H-5 in 1931 and 1932.

The large production of deep trap nets in H-5 and H-6 was made at the expense of the reserve stock rather than of a population of recent migrants. The generally low output of whitefish in southern Lake Huron prior to the introduction of the deep trap net can be attributed to a low fishing intensity. Gill nets, comparatively ineffective gear for the capture of whitefish, accounted for the bulk of the catch (appendix B). Apparently the relatively few pound nets were fished either at the wrong localities or depths to produce large quantities of whitefish. Actually, suitable localities for whitefish pound nets are scarce in southern Lake Huron.

WHITEFISH FISHERY OF LAKE MICHIGAN, 1929-1939

The most important difference between the histories of the whitefish fisheries of Lakes Michigan and Huron, 1929-1939, lies in the relatively limited development of the deep-

trap-net fishery in the former lake. With the exception of the deep-trap-net fishery out of Grand Haven, Mich., in 1934 (the deep trap net was the dominant gear for the production of whitefish in M-7 in that year), significant operations with this gear were confined to the extreme northern portion of the lake (M-1, M-2, and M-3). Deep trap nets were introduced into M-1 and M-3 in 1930 and into M-2 in 1931. Even in these northern districts the place of the deep trap net in the fishery resembled that which it occupied in northern Lake Huron rather than in central and southern Lake Huron. At no time did the deep trap net become the dominant gear for the capture of whitefish in the Green Bay area (M-1). In M-2 and M-3 deep trap nets led other gears in the production of whitefish in only two years (1932 and 1933 in both districts). The use of deep trap nets in the Michigan waters of Lake Michigan became illegal after 1935.²⁸

The fact that the deep trap net did not disturb the whitefish fishery as seriously in Lake Michigan as in Lake Huron makes it possible to follow a more or less natural course of events subsequent to an abnormal increase in abundance. Comparisons with the data on the whitefish fishery of Lake Huron should prove particularly instructive.

FLUCTUATIONS IN THE PRODUCTION OF WHITEFISH IN LAKE MICHIGAN

The increase in the catch of whitefish that characterized the late 1920's and early 1930's in the various waters of the Great Lakes got under way early in Lake Michigan.²⁹ Production exceeded 2 million pounds in 1927 and was nearly 3 million pounds in 1928.

TABLE 13.—*Production of whitefish in pounds according to gear in the State of Michigan waters of Lake Michigan, 1929-1939*

[Percentages of annual yield in parentheses]

Year	Production in gear				Total annual production	Increase or decrease
	Large-mesh gill net	Deep trap net	Pound net	Other		
1929-----	{ 2,244,093 (52.3)	-----	2,032,083 (47.4)	11,693 (0.3)	{ 4,287,869	+1,331,723
1930-----	{ 2,339,162 (48.6)	135,634 (2.8)	2,328,326 (48.4)	9,703 (0.2)	{ 4,812,825	+524,956
1931-----	{ 1,986,579 (51.9)	408,209 (10.7)	1,421,576 (37.2)	7,619 (0.2)	{ 3,823,983	-988,842
1932-----	{ 1,564,505 (46.9)	856,804 (25.7)	890,667 (26.7)	20,308 (0.6)	{ 3,332,284	-491,699
1933-----	{ 1,307,943 (58.4)	440,090 (19.7)	485,187 (21.7)	2,620 (0.1)	{ 2,235,840	-1,096,444
1934-----	{ 1,001,074 (51.8)	398,635 (20.6)	531,070 (27.5)	1,399 (0.1)	{ 1,932,178	-303,662
1935-----	{ 911,079 (63.6)	211,246 (14.8)	301,367 (21.0)	8,032 (0.6)	{ 1,431,724	-500,454
1936-----	{ 635,284 (72.5)	-----	240,508 (27.4)	619 (0.1)	{ 876,411	-555,313
1937-----	{ 709,515 (74.9)	-----	236,527 (25.0)	825 (0.1)	{ 946,867	+70,456
1938-----	{ 765,416 (68.5)	-----	351,447 (31.5)	216 (0.0)	{ 1,117,079	+170,212
1939-----	{ 482,801 (57.5)	-----	356,488 (42.4)	567 (0.1)	{ 839,856	-277,223
Average-----	{ 1,267,950 (54.4)	222,784 (9.6)	834,113 (35.8)	5,782 (0.2)	{ 2,330,629	-----

²⁸ Limited operations have been carried on in the northern Michigan waters since 1935, with a modified deep trap net in which the crib or pot extends to the surface of the water and is open at the top. This arrangement has qualified the nets for legal definition as pound nets with which gear they have been grouped in the preparation of this report.

²⁹ In this section the terms, "Lake Michigan" and "the entire lake," refer to the State of Michigan waters only.

In 1929, the first year for which detailed statistics are available, the catch of whitefish (4,288,000 pounds) was greater than that of any previous year, except 1889, for which there are usable records (table 1). The increase over the take for 1928 was 1,332,000 pounds (table 13). A further rise of 525,000 pounds in 1930 brought the yield of whitefish in Lake Michigan to the peak of 4,813,000 pounds.

Whitefish production declined continually throughout the next 6 years. The decreases were large (average of 656,000 pounds per year). In two years (1931 and 1933) the drop in catch amounted to roughly a million pounds. In three years (1932, 1935, and 1936) the decreases were approximately a half million pounds. The smallest drop in production (304,000 pounds) in the 6-year period occurred in 1934.

The 1931-1936 decline in catch was followed by increases in 1937 (70,000 pounds) and 1938 (170,000 pounds). A new drop of 277,000 pounds in 1939 carried the yield to a level that was only a little above the lowest recorded for any previous year (806,000 in 1920).

Great as the decline in production was in Lake Michigan, the yield in 1939 amounted to 17.5 percent of the 1930 maximum as compared with a 1939 catch in Lake Huron that was only 6.2 percent of the 1931 peak in that lake.

The records of the production of whitefish in deep trap nets (tables 13 and 14) confirm the earlier statement that the gear failed by far to become as important in Lake Michigan as in Lake Huron. In Lake Michigan the deep trap net accounted for only 25.7 percent of the total catch in 1932, the year of its greatest success. This percentage was less than that of pound nets (26.7 percent) and was far below the percentage for gill nets (46.9 percent). In fact, the total quantity of whitefish taken by deep trap nets in Lake Michigan in their 6 years of operation (1930-1935) was less than the amount taken by the same gear in Lake Huron in each of the single years, 1932 and 1933. The gill net was the most important gear for the capture of whitefish throughout the 11-year period and accounted for more than 50 percent of the total yield in 9 years (average of 54.4 percent for 1929-1939). With equal consistency the pound net held second rank, and accounted for 35.8 percent of the 1929-1939 take.

TABLE 14.—*Production of whitefish in pounds in deep trap nets in Lake Michigan, 1930-1935 (use of deep trap nets illegal after July 1, 1935)*

[In parentheses, the deep-trap-net production expressed as a percentage of the total whitefish production]

District or area	Production in deep trap nets in year						Total
	1930	1931	1932	1933	1934	1935	
M-1.....	{ 37,655 (3.5)	111,523 (9.3)	191,979 (21.1)	77,161 (32.4)	56,918 (21.6)	22,783	498,019
M-2.....		{ 13,645 (16.7)	59,303 (61.0)	30,753 (72.7)	11,580 (43.1)	3,621	118,902
M-3.....	{ 97,454 (4.0)	273,282 (19.8)	596,246 (40.0)	318,260 (35.7)	251,012 (32.9)	177,374	1,713,628
M-4.....		{ 174 (0.2)	1,218 (1.5)	1,569 (3.1)	249 (0.5)	4,389	7,599
Northern Lake Michigan (M-1, M-2, M-3, and M-4).....	{ 135,109 (3.6)	398,624 (14.5)	848,746 (33.0)	427,743 (35.0)	319,759 (29.1)	208,167	2,338,148
Central Lake Michigan (M-5).....			{ 3,797 (0.7)	3,482 (0.7)			7,279
M-6.....	{ 525 (0.2)	8,877 (3.5)	173 (0.2)	2,625 (6.0)	3,920 (10.5)		16,120
M-7.....		{ 347 (0.3)	3,819 (8.0)	6,240 (4.0)	74,956 (39.3)	3,079	88,441
M-8.....		{ 361 (0.3)	269 (0.4)				630
Southern Lake Michigan (M-6, M-7, and M-8).....	{ 525 (0.1)	9,585 (1.9)	4,261 (2.2)	8,865 (1.8)	78,876 (14.8)	3,079	105,191
Lake Michigan (all 8 districts).....	{ 135,634 (2.8)	408,209 (10.7)	856,804 (25.7)	440,090 (19.7)	398,635 (20.6)	211,246	2,450,618

The deep trap net became the dominant gear for the taking of whitefish in only three (M-2, M-3, and M-7) of the eight districts of Lake Michigan (table 14 and appendix B), and maintained that position in the first two districts only 2 years (1932 and 1933) and in M-7 only 1 year (1934). With the exception of the fishery in M-7 in 1934, deep trap nets were operated only sporadically in waters south of M-3.

Although the actual yield of whitefish in each district and the percentage distribution among the several districts of the total for the lake both varied rather widely in Lake Michigan during the period, 1929-1939 (table 15), there is no evidence of a shifting of the center of production comparable to that which took place in Lake Huron. For example, M-3 did not relinquish once its position as the most productive district of the lake; neither did northern Lake Michigan (M-1, M-2, M-3, and M-4) fail in any year to account for more than 50 percent of the catch of the entire lake.

TABLE 15.—Total annual production of whitefish in pounds in the different districts and areas of the State of Michigan waters of Lake Michigan, 1929-1939

[Each total is expressed also as the percentage (in parentheses) of the production of the entire lake]

District or area	Total whitefish production in year											Average
	1929	1930	1931	1932	1933	1934	1935	1936	1937	1938	1939	
M-1-----	{ 1,139,628 (26.6)	{ 1,075,748 (22.4)	{ 1,194,969 (31.3)	{ 910,106 (27.3)	{ 238,169 (10.7)	{ 263,005 (13.6)	{ 174,637 (12.2)	{ 90,203 (10.3)	{ 104,889 (11.1)	{ 354,235 (31.7)	{ 237,509 (28.3)	{ 525,736 (22.6)
M-2-----	{ 90,019 (2.1)	{ 100,625 (2.1)	{ 81,618 (2.1)	{ 97,248 (2.9)	{ 42,277 (1.9)	{ 26,858 (1.4)	{ 46,264 (3.2)	{ 46,465 (5.3)	{ 31,497 (3.3)	{ 24,221 (2.2)	{ 15,402 (1.8)	{ 54,772 (2.3)
M-3-----	{ 2,202,064 (51.3)	{ 2,460,656 (51.1)	{ 1,380,450 (36.1)	{ 1,489,472 (44.7)	{ 890,899 (39.8)	{ 761,831 (39.4)	{ 749,666 (52.4)	{ 445,967 (50.9)	{ 450,615 (47.6)	{ 497,776 (44.6)	{ 425,495 (50.7)	{ 1,068,627 (45.9)
M-4-----	{ 72,629 (1.7)	{ 84,119 (1.7)	{ 84,253 (2.2)	{ 78,771 (2.4)	{ 51,010 (2.3)	{ 48,369 (2.5)	{ 47,978 (3.3)	{ 56,234 (6.4)	{ 43,866 (4.6)	{ 29,249 (2.6)	{ 31,767 (3.8)	{ 57,113 (2.4)
Northern Lake Michigan (M-1, M-2, M-3, & M-4)	{ 3,504,340 (81.7)	{ 3,721,148 (77.3)	{ 2,741,290 (71.7)	{ 2,575,597 (77.3)	{ 1,222,355 (54.7)	{ 1,100,063 (56.9)	{ 1,018,545 (71.1)	{ 638,869 (72.9)	{ 630,867 (66.6)	{ 905,481 (81.1)	{ 710,173 (84.6)	{ 1,706,248 (73.2)
Central Lake Michigan (M-5)	{ 284,820 (6.6)	{ 280,701 (5.8)	{ 580,536 (15.2)	{ 558,573 (16.8)	{ 529,697 (23.7)	{ 298,497 (15.5)	{ 208,807 (14.6)	{ 198,801 (22.7)	{ 267,385 (23.3)	{ 189,658 (17.0)	{ 97,268 (11.6)	{ 317,686 (13.6)
M-6-----	{ 103,397 (2.4)	{ 222,148 (4.6)	{ 252,015 (6.6)	{ 85,080 (2.5)	{ 43,181 (1.9)	{ 37,450 (1.9)	{ 24,861 (1.7)	{ 14,063 (1.6)	{ 11,100 (1.2)	{ 6,787 (0.6)	{ 4,653 (0.5)	{ 73,158 (3.2)
M-7-----	{ 139,690 (3.3)	{ 447,760 (9.4)	{ 107,206 (2.8)	{ 47,934 (1.4)	{ 157,699 (7.1)	{ 190,582 (9.9)	{ 30,506 (2.2)	{ 5,212 (0.6)	{ 8,017 (0.8)	{ 1,137 (0.1)	{ 1,537 (0.2)	{ 103,389 (4.4)
M-8-----	{ 255,822 (6.0)	{ 141,068 (2.9)	{ 142,936 (3.7)	{ 65,100 (2.0)	{ 282,908 (12.6)	{ 305,586 (15.8)	{ 149,005 (10.4)	{ 19,466 (2.2)	{ 29,498 (3.1)	{ 14,016 (1.2)	{ 26,225 (3.1)	{ 130,148 (5.6)
outhern Lake Michigan (M-6, M-7, and M-8)	{ 498,909 (11.6)	{ 810,976 (16.9)	{ 502,157 (13.1)	{ 198,114 (5.9)	{ 483,788 (21.6)	{ 533,618 (27.6)	{ 204,372 (14.3)	{ 38,741 (4.4)	{ 48,615 (5.1)	{ 21,940 (1.9)	{ 32,415 (3.8)	{ 306,695 (13.2)
Lake Michigan (all 8 districts)	4,287,869	4,812,825	3,823,983	3,332,284	2,235,840	1,932,178	1,431,724	876,411	946,867	1,117,079	839,856	2,330,629
Percentage of average	184	206	164	143	96	83	61	38	41	48	36	-----

Nevertheless, the relative importance of the districts varied considerably. M-3 produced as little as 36.1 percent (1931) and as much as 52.4 percent (1935) of the total catch of whitefish in the lake. In M-1, the district that ranked second in average yield, the percentages ranged from 10.3 (1936) to 31.7 (1938). The district that ranked third in average production (M-5) yielded from 5.8 percent (1930) to 28.3 percent (1937) of the total for the lake.

The percentage contributions of the less important districts varied relatively more widely than did those for the more productive areas. The greatest relative variation occurred in M-7 which produced 9.9 percent of the 1934 total but only 0.1 percent of the 1938 catch. However, among the five districts that each accounted for less than 10 percent of the 1929-1939 average only one (M-8) produced more than 10 percent of

the total for the lake in any single year (percentages of 12.6, 15.8, and 10.4 in 1933, 1934, and 1935, respectively).

Comparison of later and earlier production of whitefish in the various districts of Lake Michigan (tables 15 and 16) reveals that M-3 contributed an even higher percentage of the total for the lake in 1891-1908 (59.5 percent) than in 1929-1939 (45.9 percent). M-2 and M-4 also accounted for higher percentages of the total in the earlier period (7.4 and 7.3 percent, respectively, as compared with 2.3 and 2.4 percent). However, the percentages for these two districts may be too high for the years, 1891-1908. As stated in footnote 23, the division of the catches for the early period was based on the home ports of the fishermen, not necessarily on the actual location of their fishing grounds. In recent years, at least, numbers of fishermen who operate from ports of M-2 and M-4 have done part of their fishing in other districts (chiefly in M-3). It is believed that the data for the remaining districts were not affected greatly by the separation of the catch of the earlier years according to the port from which the fishermen operated.

TABLE 16.—*Production of whitefish in pounds in Lake Michigan according to statistical districts, 1891-1908*

Year	Statistical district								Total
	M-1	M-2	M-3	M-4	M-5	M-6	M-7	M-8	
1891	78,140	237,000	1,521,101	214,580	290,100	41,050	17,100	5,500	2,404,571
1892	148,600	325,650	1,477,412	168,725	329,300	41,100	11,000	20,615	2,522,402
1893	123,150	83,000	1,326,900	137,050	233,600	19,500	27,500	25,100	1,975,800
1894	89,050	41,100	801,750	146,500	147,300	8,730	31,450	29,925	1,295,805
1895	71,850	18,500	631,550	109,990	138,000	7,400	21,150	24,300	1,022,740
1896	88,600	148,000	863,400	86,600	210,750	10,000	13,350	26,600	1,447,300
1897	83,570	180,000	1,762,900	84,300	261,700	13,700	6,053	26,730	2,418,953
1898	85,050	302,100	1,504,900	84,200	303,000	16,700	6,550	17,600	2,320,100
1899	111,560	104,100	1,040,870	87,500	249,600	12,350	2,800	25,100	1,633,880
1900	83,350	140,500	961,800	104,000	292,000	16,100	3,100	24,750	1,625,600
1901	97,700	146,100	1,372,600	148,700	278,200	8,700	8,900	18,650	2,079,550
1902	140,150	177,500	1,739,800	200,500	429,000	10,000	3,400	23,000	2,723,350
1903	228,200	166,000	1,369,400	148,500	319,500	17,100	6,200	29,700	2,284,600
1904	283,000	158,000	1,337,000	282,500	338,000	33,000	19,100	51,100	2,501,700
1905	348,000	184,000	1,246,800	218,000	338,500	62,600	73,500	98,700	2,570,100
1906	291,800	89,500	1,387,700	322,300	322,500	77,300	170,300	159,300	2,820,700
1907	291,700	179,000	1,689,500	244,100	330,000	139,300	265,500	134,700	3,273,800
1908	222,500	289,400	1,793,155	148,424	337,116	83,700	89,800	142,000	3,106,095
Average	159,221	164,969	1,323,808	163,137	286,009	34,352	43,153	49,076	2,223,725
Percentage	7.2	7.4	59.5	7.3	12.9	1.6	1.9	2.2	

M-1, M-5, M-6, M-7, and M-8 yielded smaller percentages of the total catch of whitefish in 1891-1908 than in 1929-1939. Especially noteworthy are the comparative yields for M-1 which accounted for only 7.2 percent of the early total catch as against 22.6 percent of the recent production. The change was not large in M-5 (12.9 percent in the early period; 13.6 percent in the recent). The percentages were considerably lower in 1891-1908 than in 1929-1939 for all three districts (M-6, M-7, and M-8) of southern Lake Michigan (1.6, 1.9, and 2.2 percent as compared with 3.2, 4.4, and 5.6 percent).

Despite the changes just described in the percentage distribution of the catch of whitefish according to district, the most productive areas of the earlier years seem to be in general the best areas of recent years. This conclusion is supported by the following comparison of regions of the lake:

Area	Percentage of total whitefish production	
	1891-1908	1929-1939
Northern Lake Michigan (M-1, M-2, M-3, M-4)	81.4	73.2
Central Lake Michigan (M-5)	12.9	13.6
Southern Lake Michigan (M-6, M-7, M-8)	5.7	13.2

CHANGES IN PRODUCTION IN LAKE MICHIGAN AS RELATED TO
FLUCTUATIONS IN THE ABUNDANCE OF WHITEFISH
AND IN THE INTENSITY OF THE FISHERY

In Lake Michigan as in Lake Huron the abundance of whitefish was abnormally high near the beginning of the 1929-1939 period. The peak of abundance occurred a year or two earlier in the more productive areas of Lake Michigan than in Lake Huron. The abundance of whitefish was greater in 1929 than in any other of the 11 years in each of the four districts of northern Lake Michigan, a region that accounted for 73.2 percent of the 1929-1939 production. The maximum abundance occurred in 1929 in M-8 also. The large increase in catch in 1929 (table 1) suggests strongly that the abundance in this year was greater than that in 1928 and hence constituted the maximum for the modern fishery. (Certainty on this point is not possible as the intensity of the fishery in 1928 is unknown.) The maximum abundance of the 1929-1939 interval occurred later in the remaining districts (1930 in M-6 and M-7, 1931 in M-5). However, these districts were relatively far less important in the fishery of the entire lake than were those in which 1929 was the year of peak abundance. Lake Michigan resembles Lake Huron again in that a decline from the high level of abundance that existed early in the period was to be expected.

These resemblances between the data for Lake Michigan and Lake Huron are fortunate, as they make possible a comparison of the course of the decline in Lake Michigan, where the whitefish fishery was not disturbed violently by the use of deep trap nets, and in Lake Huron where the introduction and widespread use of that new and efficient gear brought about an utterly chaotic condition in the fishery. Accordingly, comparisons of data for Lakes Michigan and Huron are emphasized in the present section.

Several reasons may be advanced to account for the failure of the deep-trap-net fishery to develop as extensively in Lake Michigan as in Lake Huron: (1) no extensive or good whitefish grounds are found in Lake Michigan south of Frankfort; (2) pound-netters and gill-netters rather than trap-netters were dominant on Lake Michigan and opposed the use of deep trap nets (the Lake Huron deep-trap-netters who entered M-7 in 1934 were driven out by local fishermen; shortly thereafter the Lake

TABLE 17.—*Annual fluctuation in the catch of whitefish per unit of fishing effort of gill nets, deep trap nets, and pound nets in the various districts of Lake Michigan, 1929-1939*

District	1929	1930	1931	1932	1933	1934	1935	1936	1937	1938	1939	Average
Pounds of whitefish per 10,000-foot-lift of gill nets												
M-1-----	183.4	150.0	131.0	116.3	71.4	100.2	105.2	76.5	71.7	119.7	74.0	109.0
M-2-----	69.4	63.8	44.3	27.0	15.3	19.5	49.4	43.0	32.1	26.2	24.4	37.7
M-3-----	138.9	131.6	87.6	89.9	70.4	74.0	85.8	59.0	54.6	48.6	47.3	80.7
M-4-----	52.0	50.1	60.0	48.2	37.7	29.4	34.5	48.3	25.7	25.3	25.8	39.7
M-5-----	103.9	85.8	127.1	110.6	104.1	78.4	56.5	57.1	60.2	46.9	31.3	78.4
M-6-----	55.0	65.4	75.6	40.1	37.5	31.9	31.5	14.5	22.6	14.9	17.0	36.9
M-7-----	132.5	161.5	72.8	92.4	193.1	133.3	156.5	128.8	133.1	76.4	71.0	122.9
M-8-----	156.7	117.6	111.6	81.5	160.2	141.9	102.0	48.7	75.1	70.8	79.1	104.1
Pounds of whitefish per lift of one deep trap net												
M-1-----		131.7	100.2	118.0	54.6	74.6	91.1					95.0
M-2-----			184.4	257.5	120.6	68.1	43.1					134.8
M-3-----		163.7	137.2	164.9	97.0	121.8	94.6					128.2
M-7-----						118.2						118.2
Pounds of whitefish per lift of one pound net												
M-1-----	113.2	88.7	104.5	74.1	41.0	56.0	41.8	47.6	38.0	53.9	63.0	65.6
M-2-----	105.2	85.9	217.1									136.1
M-3-----	153.3	148.8	96.0	80.0	85.6	98.5	92.4	85.3	81.5	80.0	75.6	97.9
M-4-----	73.4	71.0	57.7	63.3	67.7	63.0	54.3	56.7	63.6	31.5	40.7	58.4
M-5-----	123.1	134.2	159.2	106.8	145.0	71.4	73.6	60.5	65.2	84.1	53.9	97.9
M-6-----		261.7	126.9	55.2	26.6	41.2	34.2	84.7		121.8	55.0	89.7
M-7-----	102.9	195.4	59.8	25.7	39.4	61.1	11.0	8.8	13.1	12.7	9.2	49.0
M-8-----		243.1	146.0		37.6	73.7	29.0	54.1	70.1		13.4	83.4

Michigan fishermen were able to abolish the net from their waters by law); (3) the summer aggregation of whitefish occurs in shallower water in Lake Michigan than in Lake Huron and hence the Lake Michigan fish never moved beyond the reach of pound nets to the same degree as did those in Lake Huron; (4) the deep-water population of whitefish available to the deep trap nets was less dense in Lake Michigan than in Lake Huron, hence in contrast to the situation in Lake Huron the deep-trap-net lifts did not always average much larger than those of the pound nets. (See, for example, M-1 and M-2 for 1931, table 17.)

Although the deep trap net usually took more whitefish per lift than did the pound net in Lake Michigan, and from this point of view may be considered to have been very effective and successful, in no district of the lake did the catch per lift of deep trap nets approach the level that it attained in the four southerly districts of Lake Huron (tables 11 and 17). The average catch per lift of deep trap nets in Lake Michigan reached values of 257.5 pounds in M-2 in 1932 and 184.4 pounds in the same district in 1931. Operations were limited, however, in M-2. In M-1 and M-3, where deep-trap-net operations were more extensive, the greatest average catches per lift were 131.7 pounds (M-1 in 1930) and 164.9 pounds (M-3 in 1932). These values were far below the greatest averages in the districts of central and southern Lake Huron (402.5 to 476.1 pounds per lift), but compared favorably with the maxima in northern Lake Huron (167.7 pounds per lift in H-1 in 1930; 141.9 pounds per lift in H-2 in 1930). The deep trap net was relatively unsuccessful in southern Lake Michigan also, for the only significant operations with the gear (M-7 in 1934) yielded an average of 118.2 pounds of whitefish per lift.

To be sure, the deep trap net was introduced into northern Lake Michigan after the peak of abundance of the whitefish had passed. The examination of the abundance percentages of table 21 suggests that if this gear had been fished in 1929, the year of high abundance, the average catch per lift in that year most probably would have exceeded the highest yields listed in table 17 for deep trap nets in each of the northern districts. On the other hand, abundance percentages may not validly serve as an exact index to the average size of a lift since the fluctuations in the catch per lift of this gear did not always correspond with those in abundance subsequent to 1929. For example, the average catch per lift of deep trap nets in M-1 decreased in 1931 and increased in 1932 despite the fact that abundance remained practically unchanged in 1931 and fell in 1932. Again, the highest yield (257.5 pounds per lift) of the northern area occurred in a district (M-2) when abundance was normal (1932).

As the average deep-trap-net lifts were small in comparison with those of central and southern Lake Huron irrespective of how much abundance was above average, the conclusion appears valid that in northern Lake Michigan as in northern Lake Huron the deep trap net was far less successful than it was in central and southern Lake Huron.

The maximum and 1939 percentages of production, fishing intensity, and abundance in table 18 have been computed with respect to average conditions in 1929-1939. The corresponding estimates for Lake Huron (table 7) were made with reference to

TABLE 18.—Maximum and 1939 production and abundance of whitefish and maximum and 1939 fishing intensity for whitefish

[Expressed as percentages of the average 1929-1939 values in each statistical district of Lake Michigan]

District	Year of maximum production	Production		Year of maximum intensity	Intensity		Year of maximum abundance	Abundance	
		Maximum	1939		Maximum	1939		Maximum	1939
M-1	1931	227	45	1931	196	65	1929	170	81
M-2	1930	184	28	1932	180	41	1929	169	69
M-3	1930	230	40	1930	159	65	1929	166	67
M-4	1931	148	56	1931	127	88	1929	127	66
M-5	1931	183	31	1932	129	77	1931	162	41
M-6	1931	345	7	1931	242	16	1930	209	53
M-7	1930	433	1	1930	271	7	1930	222	33
M-8	1934	235	20	1934	215	34	1929	151	71

conditions in the single year, 1929. The figures for this year were taken as the most nearly "normal" data available (p. 323). The computation of the above percentages for Lake Michigan also with respect to 1929 conditions would not have been valid because production, abundance, and almost certainly fishing intensity, as well, were above normal in Lake Michigan in that year. On the other hand, the data for the period, 1929-1939, were not greatly, if at all, distorted by the deep-trap-net fishery in Lake Michigan. Furthermore, these 11 years included periods of high, moderate, and low production and apparently also periods of high, moderate, and low abundance and fishing intensity. Consequently, the 11-year averages have been taken as the most nearly normal bases available for the estimation of the maximum and 1939 percentages of production, fishing intensity, and abundance for the Lake Michigan whitefish. It is believed that this variation of procedure has made the data of tables 7 and 18 as nearly comparable as is possible.

In comparison with Lake Huron the maxima of yields in Lake Michigan were relatively small. The maximum exceeded 3 times the assumed normal in only two districts (433 percent in M-7 and 345 percent in M-6). Of the remaining six districts the maximum production was greater than twice the normal in three (M-1, M-3, and M-8), was between $1\frac{1}{2}$ and 2 times the normal in two (M-2 and M-5), and was less than $1\frac{1}{2}$ times the normal in one (M-4). In Lake Huron, on the contrary, the relatively lowest maximum yield was 263 percent of the 1929 catch (H-1) and the maxima in the remaining districts ranged from 317 in H-2 to as high as 2,662 in H-5. This comparison lends additional strong support to the belief that the use of the deep trap net brought about an excessive increase in yield in Lake Huron, especially in the four southern districts.

The maxima of fishing intensity were relatively lower in Lake Michigan than were the maxima of production. The peak fishing intensity was more than twice the normal only in southern Lake Michigan (M-6, M-7, and M-8). The five remaining percentages were all below 200, and two of them (M-4 and M-5) were less than 150. In Lake Huron the maximum percentage was more than twice the normal in every district; in the four southerly districts the maxima ranged from roughly 4 to 42 times the normal. Again the comparison of data for Lake Michigan and Lake Huron supports the earlier conclusion, namely, that the deep-trap-net operations led to an abnormally increased fishing intensity in Lake Huron with the increase greatest in the central and southern regions of the lake.

The maxima of abundance of whitefish were relatively higher in Lake Michigan than in Lake Huron. In two districts the percentages exceeded 200 (M-6 and M-7); of the remaining six districts the percentages were above 150 in five and below 150 in only one. The corresponding percentages for Lake Huron were all below 150. These low values of the maximum abundance of whitefish in Lake Huron suggest the possibility that abundance in 1929, the year taken as normal, may have been somewhat above normal as well as above the Lake Huron average for 1929-1939. An alternative explanation is offered by the possibility that, in some districts at least, a higher maximum abundance might have been attained if fishing intensity and production had been less.

The estimates of the 1939 conditions in Lakes Michigan and Huron in relation to the assumed "normals" for the lakes provide further striking comparisons. Production was at a low level in both lakes in 1939. In Lake Michigan, however, only two districts of eight had yields below 20 percent of normal, whereas in Lake Huron three of the six districts were below that level. Three of the Lake Michigan districts had percentages of 40 or above; in Lake Huron the only production greater than 40 percent of normal (46 in H-6) was made possible by reason of a fishing intensity that was more than 4 times the normal.

Fishing intensities in 1939 were generally relatively lower in Lake Michigan than in Lake Huron. In five of six districts of Lake Huron the intensity of the fishery for whitefish was 50 percent or more of the 1929 "normal"; in 2 districts (H-5 and H-6) the intensity in 1939 was more than 4 times the normal. The intensity of the whitefish fishery in Lake Michigan was above 50 percent of normal in only four of eight districts and was only 88 percent in M-4, the district with the most intensive fishery.

The comparison of the relative abundance of whitefish in Lakes Michigan and Huron in 1939 provides an explanation for the fact that the percentages for production were the higher in Lake Michigan in that year despite a relatively more intensive fishery in Lake Huron. The abundance of whitefish was below normal in 1939 in every district of Lake Michigan. However, the percentage was below 50 in only two of the eight districts (M-5 and M-7) and was below 60 in only three (M-5, M-6, and M-7). In Lake Huron, on the other hand, the abundance of whitefish was less than 50 percent of the 1929 "normal" in every district, and was so low as to suggest the virtual disappearance of the species from the four most southerly districts. Thus it seems that where the whitefish merely declined in abundance in Lake Michigan the species approached extermination in most of Lake Huron.

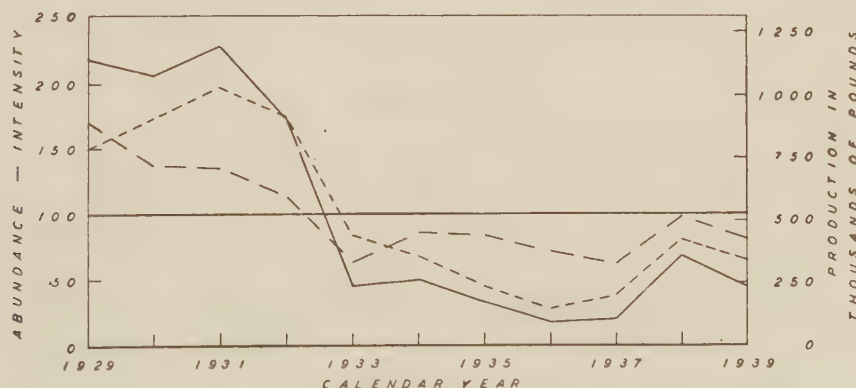
The possibility that abundance may have been above normal in 1929, the "normal" year of reference for Lake Huron, does not affect the validity of the preceding statement. If it is assumed, for example, that the abundance of whitefish in Lake Huron was 50 percent above normal in 1929, hence that the percentages for 1939 should be increased 50 percent, the following estimates are obtained of 1939 abundance as percentages of normal:

<i>District</i>	<i>Abundance</i>		<i>District</i>	<i>Abundance</i>
H-1.....	62		H-4.....	10
H-2.....	64		H-5.....	8
H-3.....	9		H-6.....	15

Even this increase leaves the percentages extremely low for the four southerly districts, although the percentages for H-1 and H-2 are raised to a point corresponding roughly with the general level in Lake Michigan.

The evidence that the use of deep trap nets in Lake Huron led to an excessively great, and ultimately ruinous, expansion of the whitefish fishery should not be taken to signify that overfishing did not take place in Lake Michigan also. The capacity for overfishing is not an exclusive characteristic of any one type of gear. Emphasis has been placed on overfishing by the deep trap net merely because its extraordinary efficiency made possible the extreme condition of overfishing observed in central and southern Lake Huron. Obviously the removal of an equal quantity of whitefish by any other gear would have proved equally disastrous.

Although the maxima of production were relatively lower in Lake Michigan than in Lake Huron, it must be considered probable that in some of the Lake Michigan districts the catch of whitefish was sufficiently great to affect adversely the abundance of the species in later years. In M-1, for example, the high fishing intensity (tables 19 and 20) that made possible the production of roughly a million pounds of whitefish in



Figures 13 to 20 show the annual fluctuations in the production (solid lines) and abundance (long dashes) of whitefish and in the intensity of the whitefish fishery (short dashes) over the period, 1929-1939, in each of the eight statistical districts of Lake Michigan (see fig. 4). In each figure the central horizontal line represents the average conditions for the 11 years, 1929-1939.

FIGURE 13.—First district, M-1.

the four consecutive years, 1929-1932 (table 15), may well have contributed to the sharp decline in abundance in 1933 (table 21). Similarly, in other districts the declines in abundance that followed years of increased fishing intensity and high yields might have been less severe had the fishery of the preceding years been less intensive. The actual detection of the possible effects of high production on the abundance of white-fish in later years is difficult, since in Lake Michigan as in Lake Huron a decline from the peak of abnormal abundance was to be anticipated whether or not extensive overfishing occurred. Furthermore, the data for Lake Michigan do not provide the sharp contrasts that made the presence and effects of overfishing in Lake Huron so easy to detect. (Compare especially the annual fluctuations in the production and fishing intensity in the various districts of the two lakes—figs. 5-10 for Lake Huron and 13-20 for Lake Michigan.)

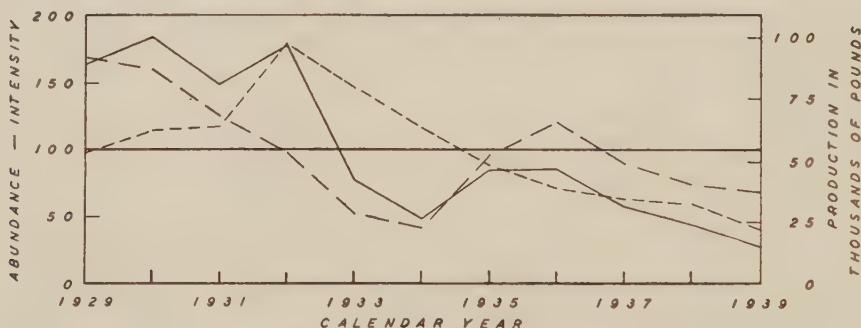


FIGURE 14.—Second district, M-2.

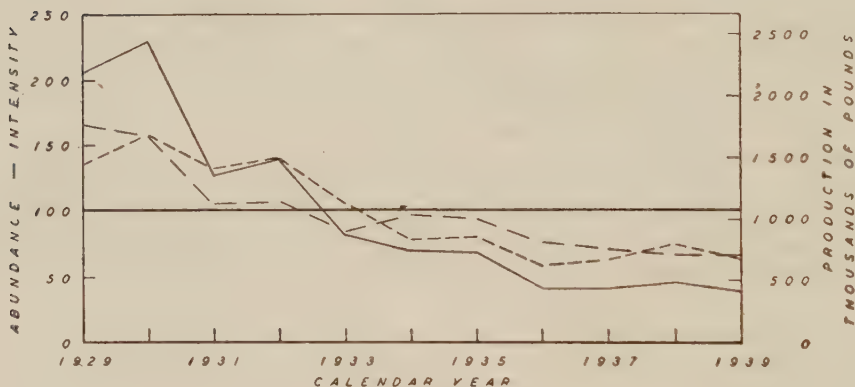


FIGURE 15.—Third district, M-3.

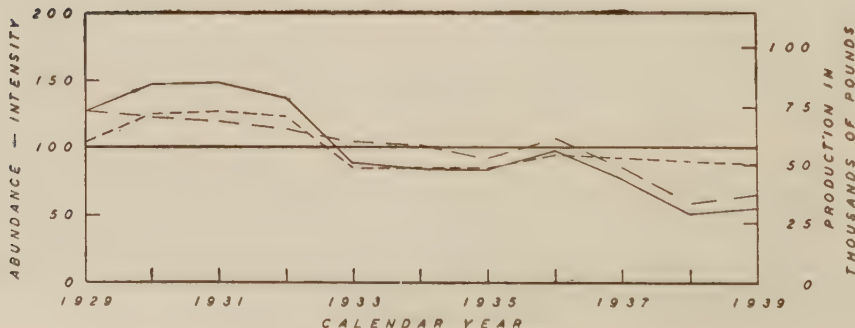


FIGURE 16.—Fourth district, M-4.

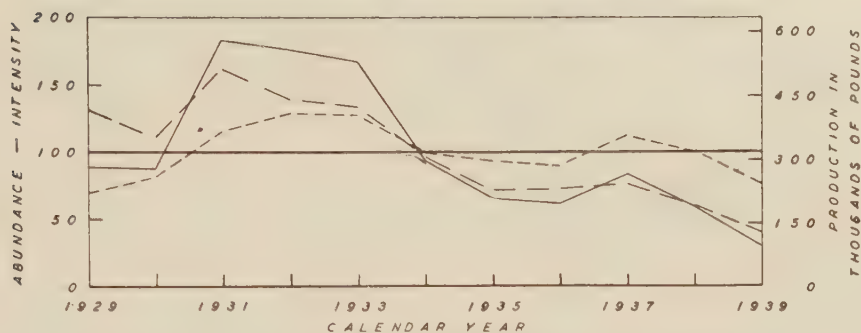


FIGURE 17.—Fifth district, M-5.

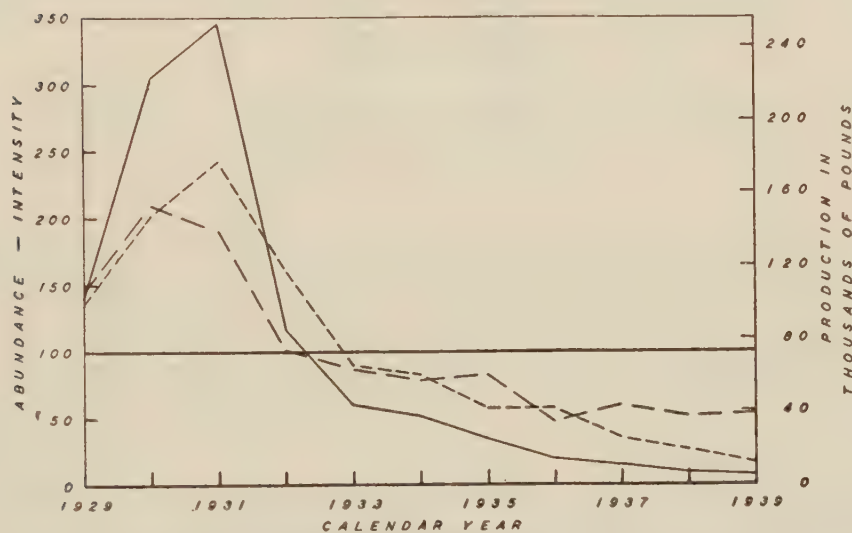


FIGURE 18.—Sixth district, M-6.

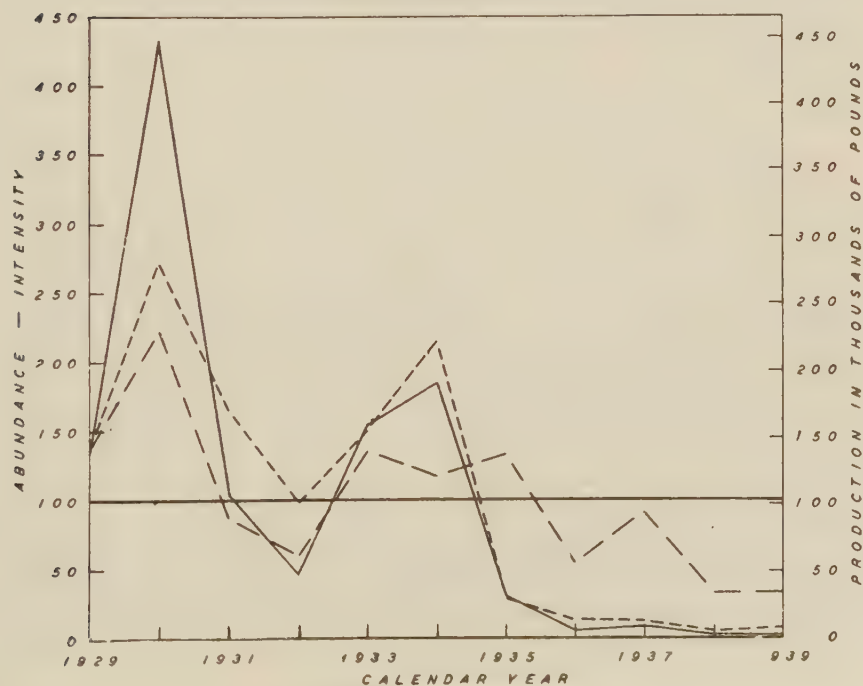


FIGURE 19.—Seventh district, M-7.

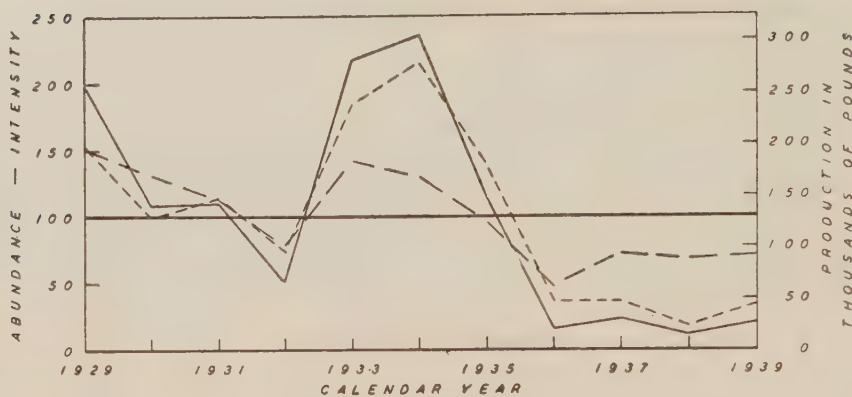


FIGURE 20.—Eighth district, M-8.

TABLE 19.—Annual fluctuations in the intensity of the fishery for whitefish in each district of Lake Michigan

[Expressed as percentages of the average 1929-1939 intensity in the district]

District	Fishing intensity as percentage of average in year										
	1929	1930	1931	1932	1933	1934	1935	1936	1937	1938	1939
M-1-----	149	173	196	174	84	68	45	28	38	80	65
M-2-----	98	115	118	180	147	117	89	71	64	60	41
M-3-----	136	159	133	141	107	79	81	59	64	76	65
M-4-----	104	125	127	123	85	85	85	95	93	90	88
M-5-----	70	82	116	129	128	100	94	90	113	101	77
M-6-----	135	201	242	160	89	82	57	57	35	26	16
M-7-----	136	271	165	98	150	214	28	14	12	5	7
M-8-----	152	99	114	74	183	215	139	36	36	18	34

TABLE 20.—Annual fluctuations in the intensity of the whitefish fishery for all eight districts of Lake Michigan combined (third row from bottom) and distribution of each year's intensity among the districts

[The average annual intensity for the entire lake, 1929-1939, is 100.0. In parentheses are the intensity values of the deep-trap-net fishery. The value of one unit is 1/1100 of the total expected catch (p. 314) of all districts, 1929-1939]

District or area	Fishing intensity in year											Total	Percentage of intensity represented by deep trap nets
	1929	1930	1931	1932	1933	1934	1935	1936	1937	1938	1939		
M-1-----	32.1	37.5 (1.2)	42.3 (4.8)	37.7 (7.0)	18.1 (6.1)	14.7 (3.3)	9.7 (1.1)	6.1	8.2	17.3	14.0	237.7 (23.5)	9.9
M-2-----	2.6	3.0	3.1 (0.7)	4.6 (2.3)	3.8 (2.6)	3.1 (1.7)	2.3 (0.8)	1.8	1.7	1.6	1.1	28.7 (8.1)	
M-3-----	63.6	74.7 (3.7)	62.6 (11.8)	66.1 (21.4)	50.4 (19.4)	37.4 (12.2)	37.9 (11.1)	27.7	30.0	35.4	30.8	516.6 (79.6)	15.4
M-4-----	2.7	3.3	3.4	3.3	2.3	2.2	2.3	2.5	2.5	2.4	2.3	29.2	
Northern Lake Michigan (M-1, M-2, M-3, & M-4)	101.0	118.5 (4.9)	111.4 (17.3)	111.7 (30.7)	74.6 (28.1)	57.4 (17.2)	52.2 (13.0)	38.1	42.4	56.7	48.2	812.2 (111.2)	13.7
Central Lake Michigan (M-5)	10.3	12.1	17.2	19.1	18.9	14.7	13.9	13.2	16.7	14.9	11.5	162.5	
M-6-----	3.4	5.1	6.1	4.0	2.3	2.1	1.5	1.4	0.9	0.6	0.4	27.3	7.4
M-7-----	4.9	9.7	5.9	3.5	5.4	17.7	1.0	0.5	0.4	0.2	0.2	39.4	
M-8-----	8.0	5.2	6.1	3.9	9.6	11.3	7.4	1.9	1.9	1.0	1.8	58.1	2.3
Southern Lake Michigan (M-6, M-7, & M-8)	16.3	20.0	18.1	11.4	17.3	21.1	9.9	3.8	3.2	1.8	2.4	125.3	
Lake Michigan (all 8 districts)	127.6	150.6 (4.9)	146.7 (17.3)	142.2 (30.7)	110.8 (28.1)	93.2 (20.1)	76.0 (13.0)	55.1	62.3	73.4	62.1	1,100.0 (114.1)	10.4
Percentage of intensity represented by deep trap nets		3.3	11.8	21.6	25.4	21.6	17.1					10.4	

¹ Intensity represented by deep-trap-net operations in M-7 in 1934 was 2.9.

TABLE 21.—*Annual fluctuations in the abundance percentages for whitefish in the various districts and areas of Lake Michigan, 1929–1939*

[Expressed as percentages of average 1929–1939 abundance. In the computation of percentages for areas of more than one district and for the entire lake the abundance percentage for each district was weighted according to the percentage of the total 1929–1939 production contributed by that district]

District or area	Abundance percentage in year										
	1929	1930	1931	1932	1933	1934	1935	1936	1937	1938	1939
M-1.....	170	137	135	113	63	86	84	71	62	98	81
M-2.....	169	161	126	99	53	42	96	121	90	74	69
M-3.....	166	158	106	108	85	98	95	77	72	68	67
M-4.....	127	123	120	114	104	102	92	107	86	59	66
Northern Lake Michigan (M-1, M-2, M-3, and M-4).....	166	150	116	109	78	93	92	78	70	77	71
Central Lake Michigan (M-5).....	132	111	162	140	134	97	72	73	77	61	41
M-6.....	144	209	190	101	86	78	82	47	59	51	53
M-7.....	136	222	86	60	135	117	133	54	91	33	33
M-8.....	151	131	113	78	142	130	96	48	72	68	71
Southern Lake Michigan (M-6, M-7, and M-8).....	144	180	123	78	126	113	105	50	75	52	54
Lake Michigan (all 8 districts).....	158	149	123	109	92	96	91	73	72	72	65

A suggestion of overfishing is provided by the data for M-7. In this district the greatest maximum yield (433 percent of the 1929–1939 average) was associated with the lowest relative abundance (33 percent) in 1939 (table 18). Abundance in 1939 was low also in M-6 (53 percent), the district with the second highest maximum production percentage (345). The maximum fishing intensity also was relatively high in both M-6 and M-7 (242 and 271, respectively). On the other hand, the 1939 abundance was low (41 percent) in M-5, where there was no indication of overfishing in 1929–1939 (maximum production, 183 percent of normal; maximum intensity, 129 percent of normal).

Although, as stated previously, overfishing cannot be disregarded as a possible contributing factor in the decline in abundance of the Lake Michigan whitefish, there can be no doubt that overfishing was relatively unimportant in Lake Michigan as compared with Lake Huron. In the discussion of the data for Lake Huron emphasis was placed on the unreasonable expansion of fishing intensity and especially on the fact that this intensity remained abnormally high even in the face of decreasing abundance. The data for Lake Michigan, on the contrary, reveal a much more rational relationship between abundance and fishing intensity (and hence between abundance and yield).

Despite certain exceptions it can be said that in the Lake Michigan districts, as a whole, periods of relatively high abundance were also periods of relatively high fishing intensity and production (tables 15, 19, and 21; figs. 13 to 20). It is true that the changes in fishing intensity tended to lag somewhat behind the changes in abundance. Commonly the peak of fishing intensity occurred a year or two later than the peak of abundance, and the subsequent decline in fishing intensity was delayed correspondingly. Nevertheless, fishing intensity and yield were above average in a large majority of the years in which the abundance of whitefish was above average, and, conversely, fishing intensity and production were below average in the majority of the years in which the abundance of whitefish was below average. There was a tendency also for the percentages of fishing intensity and catch to be greater than the abundance percentages when abundance was above average and less than the abundance percentages when abundance was below average. The curves of fishing intensity tended to lie outside (with reference to the average) the curves of abundance, and the curves of production tended to fall outside both the curves of abundance and fishing intensity.

The tendency for the Lake Michigan fishermen to regulate their fishing activities according to the abundance of whitefish is brought out further by the fact that the coefficient of correlation between the percentages of fishing intensity and abundance

over the 11-year period (88 pairs of percentages) was 0.70. For Lake Huron, where intensive fishing frequently was carried on despite a low abundance of whitefish, the coefficient of correlation between the percentages of fishing intensity and abundance (66 pairs of percentages) was only 0.23.

The statement that fishing intensity and production were better adjusted to the abundance of whitefish in Lake Michigan than in Lake Huron applies to the data for the entire lakes (table 22) as well as to the data for the individual districts. (Compare also figs. 11 and 21.) In Lake Michigan the fishing intensity for whitefish was

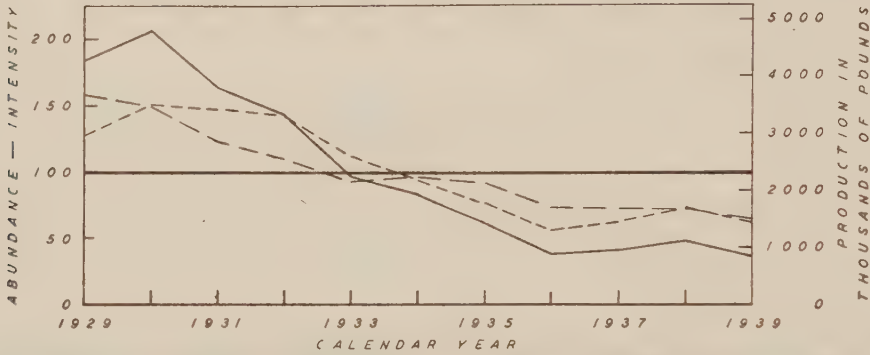


FIGURE 21.—Annual fluctuations in the production (solid line) and abundance (long dashes) of whitefish and in the intensity of the whitefish fishery (short dashes) in Lake Michigan (all eight districts combined), 1929-1939.

above average in every year in which the abundance was above average and was less than average in 6 of the 7 years in which abundance was below average. Furthermore, the intensity percentage exceeded the abundance percentage in 3 of the 4 years in which abundance was above 100 but was less than the abundance percentage in 5 of the 7 years in which abundance was below 100. Every year in which the abundance of whitefish was above average was a year of greater than average production; the catch of whitefish was below average, however, in every year in which the abundance of the species was below average. The production percentage exceeded the abundance percentage in every year in which abundance was above average, but the former was less than the latter in 6 of the 7 years with abundance below average.

TABLE 22.—Production and abundance of whitefish and the intensity of the whitefish fishery in the State of Michigan waters of Lakes Michigan and Huron

[Expressed as percentages of the 1929-1939 average]

Lake	Item	Year										
		1929	1930	1931	1932	1933	1934	1935	1936	1937	1938	1939
Michigan	Production.....	184	206	164	143	96	83	61	38	41	48	36
	Fishing intensity.....	128	151	147	142	111	93	76	55	62	73	62
	Abundance.....	158	149	123	109	92	96	91	73	72	72	65
Huron	Production.....	68	134	193	189	155	120	88	67	48	26	12
	Fishing intensity.....	46	69	100	120	155	125	139	112	100	88	46
	Abundance.....	152	195	195	140	89	77	67	61	55	38	31

Altogether different was the relationship of fishing intensity and production to the abundance of whitefish in Lake Huron. In that lake the fishing intensity was above average in 5 (exactly 100 percent in 1 year) of the 7 years in which abundance was below average; furthermore, the intensity percentage exceeded the abundance percentage in every one of these 7 years. The catch also was disproportionately high in periods of low abundance. The catch percentage exceeded the abundance percentage in

4 of the 7 years in which abundance was less than 100. The circumstance that fishing intensity was so much below the maximum in the years in which the abundance of the Lake Huron whitefish was above average should not be taken to indicate that the Lake Huron fishermen were less prompt than the Lake Michigan fishermen to take advantage of this abnormal abundance. In fact, the fishing intensity rose sharply in Lake Huron as the increase from 46 in 1929 to 100 in 1931 shows. The 1931 intensity was more than twice that of 2 years earlier. The fishing intensity in these early years of the 11-year period is represented by small percentages simply because the excessive use of deep trap nets led to a 1929-1939 average of fishing intensity that was far above a level that could reasonably be considered normal. It is doubtful whether without the use of deep trap nets the intensity would have reached the high level recorded for 1932, and much less have risen to still higher levels and maintained itself above the 1932 intensity until 1936. These considerations serve to bring out again the immensity of the overfishing that occurred in Lake Huron.

From the mass of evidence obtained from the statistical data of the whitefish fisheries of Lakes Huron and Michigan the following general conclusions may be drawn.

Lake Huron.—The deep-trap-net fishery, expansion of which was fostered by an abnormal abundance of whitefish that reached its peak in 1930-1931, was the primary cause of excessive overfishing in Lake Huron. This overfishing led to the collapse of the whitefish fishery in central and southern Lake Huron and contributed to the decline of the fishery in the northern part of the lake.

Lake Michigan.—A similar abnormal abundance of whitefish in Lake Michigan, with the peak probably in 1929, was accompanied by increases in fishing intensity and production. Although this intensive fishery may have affected adversely the later abundance of whitefish, there is no evidence of overfishing comparable to that which occurred in Lake Huron. The decline of the whitefish in Lake Michigan was pronounced but not disastrous. The difference in the course of the fishery in the two lakes can be attributed to the relatively limited use of deep trap nets in Lake Michigan.

PART III

BATHYMETRIC DISTRIBUTION OF WHITEFISH AND OF CERTAIN OTHER SPECIES IN THE SHALLOWER WATERS OF LAKES HURON AND MICHIGAN

The following sections are based on counts of whitefish and certain other species in 456 lifts of pound nets and deep trap nets in Lake Huron and 380 lifts in Lake Michigan in the years, 1931-1932. The original compilations of the data were much more detailed than those presented here. The tables showing the bathymetric distribution of the fish represent combinations of large-mesh (4 inches and larger, stretched measure) and small-mesh (less than 4 inches) nets of different dimensions, of different fishing grounds in the same general area, and of data for corresponding months in 1931 and 1932. However, these combinations were made only after a careful examination of the material demonstrated that the condensed data did not lead to conclusions that were at variance with those that would have been drawn from more detailed information.

In the main, the data have been compiled according to 10-foot depth intervals. However, for species other than the yellow pike, all lifts of nets from depths of 40 feet and less have been combined, as have also those from 41-60 feet. In deep water all lifts from more than 120 feet (more than 110 feet in Lake Michigan) have been combined. The greatest depth in which a deep trap net was set, so far as we know, was about 160 feet. This net was set in Lake Huron. Seldom were deep trap nets placed in water deeper than 140 feet. In Lake Michigan the whitefish grounds were located in much shallower water. Although a few pound nets set in more than 60 feet of water were visited and a few deep-trap-net lifts from depths of 60 feet or less were observed, for practical purposes the 60-foot contour may be considered as the line of separation of the two types of gear. The change from pound nets to deep trap nets at a depth of about 60 feet should not affect the value of the data, since we did not find any important differences in the catch of pound nets and deep trap nets that were fished in the same depth of water. All lifts observed from depths of more than 120 feet were made in Lake Huron.

As a convenience in reading the tables, asterisks have been employed to designate those depth intervals that contained the more significant peak concentrations of fish. As an additional convenience, whitefish and yellow pike frequently will be termed merely "legal" and "illegal" fish on the basis of a 2-pound and 1½-pound size limit, respectively, which limits were in effect in Michigan at the time of the investigation.

BATHYMETRIC DISTRIBUTION OF WHITEFISH IN LAKE HURON

NORTHERN LAKE HURON (CHEBOYGAN AND ROGERS CITY)

The number of lifts (20) of pound nets and deep trap nets observed in northern Lake Huron was insufficient to provide reliable data on the bathymetric distribution of the whitefish. The largest lifts of legal-sized whitefish were taken from depths of 71-80 feet in July and August and of 61-70 feet in September (table 23). The greatest numbers of illegal-sized fish occurred in lifts from 71-80 and 91-100 feet. (Only one lift from the latter depth was observed.)

ALPENA-OSSINEKE GROUNDS

Although a fairly large number (158) of pound-net and deep-trap-net lifts was examined on the Alpena and Ossineke grounds, the scarcity of data for the shallower water makes a detailed description of the depth distribution of whitefish in this area impossible (table 24). Nearly half of the lifts were from depths of 111-120 feet and the

bulk of the remainder were from depths of 81-110 feet. For no month were data available for all waters. Outstanding features of the Alpena-Ossineke data were the comparative scarcity of legal whitefish and the great abundance of undersized individuals.

TABLE 23.—*Number of legal and illegal whitefish per lift of pound nets and deep trap nets in northern Lake Huron (ports of Cheboygan and Rogers City), 1931-1932*

[Number of lifts in parentheses. Asterisks indicate concentrations]

Month	Number of legal whitefish per lift at depth (in feet)					Month	Number of illegal whitefish per lift at depth (in feet)				
	41-60	61-70	71-80	81-90	91-100		41-60	61-70	71-80	81-90	91-100
July.....		{ 20.0 (2)	51.2 (4)			July.....		{ 46.5 (2)	40.0 (4)		
August.....			{ 19.0 (2)	3.0 (2)	12.0 (1)	August.....			{ 88.0 (2)	17.5 (2)	69.0 (1)
September.....	{ 9.0 (1)	26.2 (5)	12.3 (3)			September.....	{ 6.0 (1)	5.8 (5)	5.7 (3)		
Average.....	{ 9.0 (1)	24.4 (7)	31.1* (9)	3.0 (2)	12.0 (1)	Average.....	{ 6.0 (1)	17.4 (7)	39.2* (9)	17.5 (2)	69.0 (1)

TABLE 24.—*Number of legal and illegal whitefish per lift of pound nets and deep trap nets in the Alpena-Ossineke area, 1931-1932*

[Number of lifts in parentheses. Asterisks indicate concentrations]

Month	Number of legal whitefish per lift at depth (in feet)							
	41-60	61-70	71-80	81-90	91-100	101-110	111-120	>120
May.....				{ 20.0 (1)		20.0 (1)	34.0 (23)	54.0* (4)
June.....	{ 9.8 (4)	9.0 (1)		39.0 (1)	23.0 (1)	23.7* (6)	14.7 (18)	15.0 (5)
July.....	{ 7.0 (1)		24.0 (1)	43.2* (5)	37.3 (12)	12.6 (7)	36.0* (23)	
August.....	{ 42.0 (2)	71.0 (1)	92.7* (7)	50.4 (9)	44.3 (3)	21.0 (5)	35.2* (10)	
September.....						{ 96.8 (5)	198.5* (2)	
Average.....	{ 19.6 (7)	40.0 (2)	84.2* (8)	45.6 (16)	37.8 (16)	35.0 (24)	34.5 (76)	32.3 (9)

Month	Number of illegal whitefish per lift at depth (in feet)							
	41-60	61-70	71-80	81-90	91-100	101-110	111-120	>120
May.....				{ 219.0 (1)		243.0 (1)	255.8* (23)	239.2 (4)
June.....	{ 106.0 (4)	109.0 (1)		311.0 (1)	163.0 (1)	190.0* (6)	64.2 (18)	62.8 (5)
July.....	{ 262.0 (1)		95.0 (1)	195.8* (5)	117.8 (12)	52.3 (7)	69.0* (23)	
August.....	{ 173.0* (2)	86.0 (1)	75.7 (7)	114.1* (9)	38.7 (3)	36.4 (5)	66.5* (10)	
September.....						{ 33.4 (5)	92.5* (2)	
Average.....	{ 147.4* (7)	97.5 (2)	78.1 (8)	158.5* (16)	105.8 (16)	87.4 (24)	124.7 (76)	141.2 (9)

Distribution of legal-sized whitefish.—In May the average numbers of legal whitefish taken in 111–120 feet and in “deep-water” (more than 120 feet) lifts were above those of the single lifts from 81–90 and 101–110 feet. In June, however, the average catches of the nets from the deeper water were exceeded by the catch of the 6 nets set in 101–110 feet. The 5 lifts in shallow water (41–70 feet) averaged only 9.0 and 9.8 fish for the two intervals involved. The largest average lifts in July occurred at depths of 81–90 feet (43.2) and 91–100 feet (37.3). However, the average number of fish in lifts from 111–120 feet was almost three times that of lifts from the 101–110 foot interval. The single lift in shallow water (41–60 feet) was again small (7.0 fish). The depth from which the largest lifts were made in August was shallower than that in July (71–80 feet). It is to be noted also that the average numbers of fish taken in the shallow water far exceeded the corresponding averages for June and July. In August, again, the catch of nets set at 111–120 feet was well above that of nets set at 101–110 feet. This agreement between the July and August data suggests that in late summer whitefish may be concentrated at more than one depth.³⁰ The September data cover only two intervals of depth. In this month the average number of legal whitefish per lift from 111–120 feet was twice that of nets from 101–110 feet, and in both intervals the numbers were relatively large, suggesting a return of the fish to deep water.

The data offer some evidence of an onshore movement of legal whitefish as the summer progresses. In May concentrations were greatest in the deepest water (beyond 110 feet). In June a general shift seemed to have occurred to waters between 80 and 111 feet deep, in July to waters of depths between 70 and 101 feet, and in August to depths between 60 and 91 feet.

In the averages for the entire season the number of legal fish per lift increased from shallow water to a maximum of 84.2 fish at depths of 71–80 feet. Beyond this depth interval there was a continuous decline in the average number of legal whitefish per lift.³¹

Distribution of illegal-sized whitefish.—The data on the bathymetric distribution of illegal whitefish bear considerable resemblance to those of legal fish. In both size groups the average number of fish per lift was greater at 111–120 feet than at 101–110 feet in every month but June. Furthermore, both groups appear to undertake an onshore movement as the summer progresses. A difference is found between the vertical distribution of legal and illegal whitefish in the greater abundance of the latter group in shallow water.

The averages for the entire season show heavy concentrations of young whitefish in the intervals: 41–60 feet, 81–90 feet, and more than 120 feet. These fish were least abundant in depths of 71–80 and 101–110 feet. These averages, however, are influenced by the shift in concentrations. The monthly figures indicate a heavy concentration in all depths beyond 80 feet in May, between 80 and 111 feet in June, between 80 and 101 feet in July, and in 81–90 feet in August. In September the number again increased in the 111–120 foot interval. A comparison of the seasons' averages reveals that the maximum concentration of illegal whitefish (81–90 feet) was in water 10 feet deeper than the maximum for legal fish (71–80 feet). However, legal fish did not share the inshore abundance of the smaller whitefish.

SAGINAW BAY AREA (OSCODA, EAST TAWAS, AND BAY PORT)

A total of 223 lifts of pound nets and deep trap nets was examined in the Saginaw Bay area. Despite this large total, the distribution of the lifts leaves certain depths of less than 91 feet poorly represented (table 25). With the exception of a few lifts on northerly and easterly courses out of Oscoda, the deep-trap-net lifts were made on the grounds of district H-4. (See fig. 4.) Most of the pound nets observed were in the neighborhood of East Tawas. The Saginaw Bay area differed from the Alpena-Ossineke grounds in the relatively high abundance of legal, as compared with illegal, fish.

³⁰ The evidence for more than one “concentration depth” is not strong (particularly for legal whitefish) in the Alpena-Ossineke data. The suggestion is brought out here because of the later conclusive evidence that there are two concentration zones in northeastern Lake Michigan (p. 353). No good evidence of a concentration at 111–120 feet was found in other Lake Huron waters.

³¹ The September data obscure the presence of two concentrations of legal whitefish. If the September data are excluded the average numbers of legal whitefish per lift become 18.7 at 101–110 feet and 30.3 at 111–120 feet.

TABLE 25.—*Number of legal and illegal whitefish per lift of pound nets and deep trap nets in the Saginaw Bay area (ports of Au Sable-Oscoda, East Tawas, and Bay Port), 1931-1932*

[Number of lifts in parentheses. Asterisks indicate concentrations]

Month•	Number of legal whitefish per lift at depth (in feet)								
	<41	41-60	61-70	71-80	81-90	91-100	101-110	111-120	>120
May.....						{ 1.0 (1)	23.0 (7)	30.8 (6)	93.0* (5)
June.....	{ 15.8 (5)	7.6 (9)				{ 11.0 (1)	37.3* (14)	31.2 (22)	18.6 (11)
July.....	{ 0.2 (6)	18.0 (1)			{ 71.5 (2)	87.7 (11)	129.1* (7)	45.2 (15)	84.3* (6)
August.....		{ 51.8 (5)	24.0 (3)	111.5 (4)	190.9 (12)	216.8* (12)	176.9 (15)	171.7 (15)	117.0 (10)
September.....				{ 200.0* (2)	4.0 (1)	15.5 (2)	44.0 (2)	299.8* (4)	250.5 (2)
October.....								{ 108.0 (2)	167.3* (3)
Average.....	{ 7.3 (11)	23.0 (15)	24.0 (3)	141.0 (6)	162.5* (15)	133.7 (27)	96.2 (45)	86.6 (64)	90.5 (37)

Month	Number of illegal whitefish per lift at depth (in feet)								
	<41	41-60	61-70	71-80	81-90	91-100	101-110	111-120	>120
May.....						{ 7.0 (1)	82.3* (7)	56.3 (6)	15.2 (5)
June.....	{ 30.2 (5)	14.3 (9)				{ 20.0 (1)	52.0* (14)	21.8 (22)	3.7 (11)
July.....	{ 2.3 (6)	21.0 (1)			{ 17.0 (2)	16.2 (11)	21.0* (7)	5.7 (15)	7.3* (6)
August.....		{ 25.8 (5)	47.0 (3)	99.8 (4)	150.9* (12)	115.2 (12)	47.6 (15)	30.7 (15)	13.4 (10)
September.....				{ 63.0* (2)	14.0 (1)	40.5 (2)	85.0* (2)	74.8 (4)	66.5 (2)
October.....								{ 24.5 (2)	44.0 (3)
Average.....	{ 15.9 (11)	18.6 (15)	47.0 (3)	87.5 (6)	123.9* (15)	61.8 (27)	51.9 (45)	26.7 (64)	15.1 (37)

Distribution of legal-sized whitefish.—Again there is evidence of an onshore movement of legal whitefish during the summer followed by a return to deeper water in early autumn, apparently beginning in August. (See also p. 350.) The depths of maximum concentration in the different months were: May—more than 120 feet; June and July—101-110 feet (the shift was more toward shallower water in July than in June); August—91-100 feet; September—111-120 feet; October—more than 120 feet (only two intervals represented). There were two peaks in the August data (41-60 feet and 91-100 feet) and in the September data (71-80 feet and 111-120 feet). However, the number of lifts was so small at some depths that it cannot be concluded that the whitefish were concentrated at two depth intervals. The average number of legal whitefish per lift through the entire season increased continuously from shallow water (less than 41 feet) to the maximum at 81-90 feet, declined in the next three intervals, and increased slightly at depths greater than 120 feet.

Distribution of illegal-sized whitefish.—The data on the bathymetric distribution of young whitefish indicate an onshore movement followed by an offshore movement similar to that of legal fish. The depths of maximum concentration were: May, June, and July—101-110 feet (in each succeeding month, however, the shift was toward the shallower water); August—81-90 feet; September—101-110 feet; October—more than 120 feet. In the averages for the entire season the maxima for legal and illegal fish

were in the same interval (81-90 feet). The strongest indication of two concentration zones of illegal fish is found in the scanty September data. Young whitefish were much scarcer in the shallower water of the Saginaw Bay area than at corresponding depths on the Alpena-Ossineke grounds.

HARBOR BEACH GROUNDS

The observations of 55 lifts of deep trap nets off Harbor Beach (no pound nets were observed here) were all made in the latter part of the 1932 season (table 26), when on the basis of the preceding data the whitefish would be expected to be concentrated in the deeper water. Actually here is where the deep trap nets were found in operation. Fifty of the lifts were made from depths greater than 90 feet. Consequently, no detailed description of the vertical distribution of whitefish at all depths in this area is possible. The maximum concentration of both legal and illegal whitefish occurred in the 101-110 foot interval in all three months. In the season's average the number of legal fish per lift was greater at 91-100 feet than in waters deeper than 110 feet, but the reverse relationship was found in the data for illegal whitefish. The single shallow-water lift (41-60 feet) contained no whitefish. The legal whitefish were more abundant than the illegal fish at all depths.

TABLE 26.—Number of legal and illegal whitefish per lift of deep trap nets off Harbor Beach, 1932

[Number of lifts in parentheses. Asterisks indicate concentrations]

Month	Number of legal whitefish per lift at depth (in feet)							
	41-60	61-70	71-80	81-90	91-100	101-110	111-120	> 120
August.....					{ 251.0 (1)	420.5* (2)	408.3 (4)	135.8 (5)
September.....	{ 0.0 (1)		101.0 (1)	42.0 (3)	270.5 (8)	291.7* (12)	134.2 (6)	163.0 (3)
October.....					{ 62.5 (2)	117.3* (3)	34.5 (2)	46.0 (2)
Average.....	{ 0.0 (1)		101.0 (1)	42.0 (3)	231.5 (11)	276.1* (17)	208.9 (12)	126.0 (10)

Month	Number of illegal whitefish per lift at depth (in feet)							
	41-60	61-70	71-80	81-90	91-100	101-110	111-120	> 120
August.....					{ 150.0 (1)	298.0* (2)	266.8 (4)	79.0 (5)
September.....	{ 0.0 (1)		65.0 (1)	33.3 (3)	73.2 (8)	167.2* (12)	67.7 (6)	75.3 (3)
October.....					{ 32.0 (2)	67.7* (3)	32.0 (2)	55.5 (2)
Average.....	{ 0.0 (1)		65.0 (1)	33.3 (3)	72.7 (11)	165.0* (17)	128.1 (12)	73.2 (10)

BATHYMETRIC DISTRIBUTION OF WHITEFISH IN LAKE MICHIGAN

GREEN BAY AREA (MARINETTE, ESCANABA, AND FAIRPORT)

The 30 lifts of pound nets and deep trap nets observed in the Green Bay area do not offer adequate information on the bathymetric distribution of the whitefish at any one time or on the seasonal movements of whitefish. The data of table 27, however, indicate rather clearly that legal whitefish in this region were in deeper water in September (61-80 feet) than in May (60 feet and less). Illegal whitefish were relatively numerous in May at depths less than 61 feet, and were present in large numbers also in the two lifts from the 81-90 foot interval. Few illegal whitefish were taken at any depth in September.

TABLE 27.—*Number of legal and illegal whitefish per lift of pound nets and deep trap nets in the Green Bay area (ports of Marinette, Escanaba, and Fairport), 1931-1932*

[Number of lifts in parentheses. Asterisks indicate concentrations]

Month	Number of legal whitefish per lift at depth (in feet)						
	<41	41-60	61-70	71-80	81-90	91-100	101-110
May.....	{ 61.4 (5)	{ 51.2 (5)	{ 16.0 (1)	----- -----	{ 23.5 (2)	----- -----	----- -----
September.....	{ 4.0 (1)	{ 9.8 (4)	{ 33.8 (5)	{ 68.7* (3)	----- -----	{ 4.5 (2)	{ 8.5 (2)
Average.....	{ 51.8 (6)	{ 32.8 (9)	{ 30.8 (6)	{ 68.7 (3)	{ 23.5 (2)	{ 4.5 (2)	{ 8.5 (2)

Month	Number of illegal whitefish per lift at depth (in feet)						
	<41	41-60	61-70	71-80	81-90	91-100	101-110
May.....	{ 56.0 (5)	{ 65.8 (5)	{ 11.0 (1)	----- -----	{ 183.0 (2)	----- -----	----- -----
September.....	{ 2.0 (1)	{ 3.5 (4)	{ 7.2 (5)	{ 9.7* (3)	----- -----	{ 1.5 (2)	{ 2.0 (2)
Average.....	{ 47.0 (6)	{ 38.1 (9)	{ 7.8 (6)	{ 9.7 (3)	{ 183.0 (2)	{ 1.5 (2)	{ 2.0 (2)

NORTHEASTERN LAKE MICHIGAN
(MANISTIQUE, EPOUFETTE, AND NAUBINWAY)

The data on the bathymetric distribution of the whitefish are more complete for northeastern Lake Michigan than for any other region. Not only was the number of lifts of pound nets and deep trap nets observed large (350) but these lifts were well distributed as to depth of water. Only the deep water (depths greater than 110 feet) was poorly represented, largely because few nets were set there owing to the comparative scarcity of whitefish.

Distribution of legal-sized whitefish.—Peak concentrations of legal whitefish in June occurred at 61-70 feet and 81-90 feet (table 28 and fig. 22). The average number of fish per lift in "deep water" (more than 110 feet) exceeded slightly the average in 101-110 feet but the deeper water was represented by only two lifts. There were again two peaks in July, but in this month they occurred in water 20 feet deeper (81-90 and 101-110 feet). This offshore movement was reflected also in the reduced catches of nets in all waters shallower than 71 feet. The depths of greatest concentration of legal whitefish were the same in August as in July although the small decrease in the average number of fish from nets set in 71-80 feet together with the increase in the catch per net from all deeper waters may be taken as an indication of possible further offshore movement. In September the average number of legal whitefish per lift was below the August average at all depths less than 91 feet. The single peak occurred in the 101-110 foot interval. (Nothing is known concerning the abundance of whitefish at depths greater than 110 feet in September.) The improved catches in the shallower water (less than 71 feet) in October offer evidence of a return onshore movement. In this same month the condition of two concentration zones reappeared although it was by no means pronounced.

The seasons' averages show a consistent increase in the number of legal fish per lift from shallow water (less than 41 feet) to the 81-90 foot interval, followed by a sharp decline at 91-100 feet and a rise to a second peak at 101-110 feet. The average of 7 lifts from the deepest water was about half that of lifts from the 101-110 foot interval.

Distribution of illegal-sized whitefish.—The data on the depth distribution of illegal whitefish resembled in general those for legal fish. Both groups were characterized by

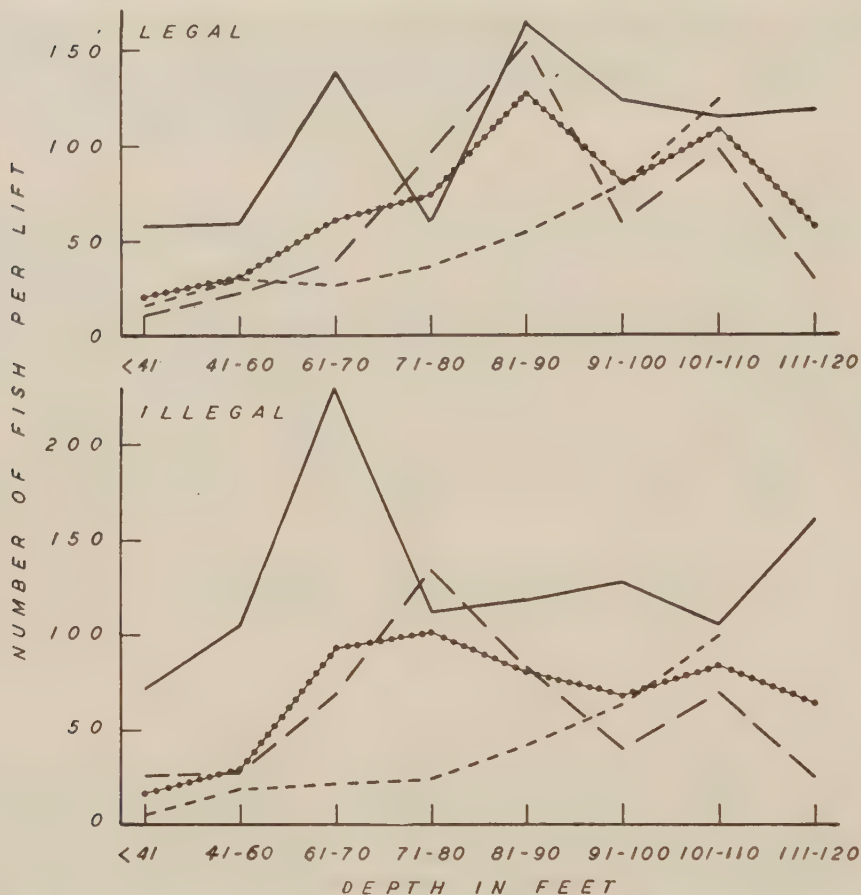


FIGURE 22.—Bathymetric distribution of legal- and illegal-sized whitefish in northeastern Lake Michigan as determined from the average numbers of fish per lift of pound nets and deep trap nets. June, solid line; July-August, long dashes; September-October, short dashes; entire season, dotted line.

two concentration zones in every month but September, and both showed an offshore movement of the fish during the summer. The two groups of data differed at times, however, as to the actual depths of the concentrations. A further difference lay in the lack of evidence of an onshore movement of illegal fish in October.

The June averages of the number of undersized whitefish per lift had peaks at 61-70 and 91-100 feet. With the illegal, as with the legal, fish the average for the deepest water (more than 110 feet) exceeded that for the 101-110 foot interval. The inshore concentration coincided with that of the legal fish, but the offshore concentration occurred 10 feet deeper. In July the movement toward deeper water increased the depth of each of the concentration zones of illegal whitefish by only 10 feet as compared with 20 feet for the legal fish. The depth intervals of the concentration zones remained unchanged in August although the decrease in the average number of fish per lift in all depths less than 91 feet points toward further offshore movement. The decrease in the number of illegal fish per lift at these depths continued in September. At the same time the number per lift increased in the 91-100 foot and 101-110 foot intervals. The September data had only one peak (at 101-110 feet) but there were again two concentration zones in October. The October averages for shallow-water lifts (depths less than 71 feet), contrary to the data for legal fish, showed no tendency to increase over those for September.

The seasons' averages indicated an increase in the number of illegal whitefish per lift from shallow water (less than 41 feet) to a peak at 71-80 feet, followed by a decline to 91-100 feet, a rise to a second peak at 101-110 feet, and yet another decrease in the

TABLE 28.—*Number of legal and illegal whitefish per lift of pound nets and deep trap nets in northeastern Lake Michigan (ports of Manistique, Epoufette, and Nausubway), 1931-1932*

[Number of lifts in parentheses. Asterisks indicate concentrations]

Month	Number of legal whitefish per lift at depth (in feet)							
	<41	41-60	61-70	71-80	81-90	91-100	101-110	>110
June.....	{ 57.5 (8)	59.3 (3)	138.8* (4)	59.5 (8)	164.3* (23)	122.5 (11)	113.7 (7)	117.5 (2)
July.....	{ 10.0 (7)	17.6 (5)	39.2 (5)	104.3 (11)	140.9* (17)	58.4 (5)	92.9* (13)	7.7 (3)
August.....	{	{ 44.0 (1)	-----	90.2 (16)	162.3* (22)	59.4 (15)	100.0* (15)	63.5 (2)
September.....	{ 7.6 (20)	28.1 (9)	18.0 (3)	36.2 (13)	55.0 (14)	88.4 (17)	121.6* (8)	-----
October.....	{ 23.1 (23)	31.5 (11)	35.7 (3)	-----	52.6* (13)	49.5 (6)	122.7* (7)	-----
Average.....	{ 20.9 (58)	31.4 (29)	60.8 (15)	73.7 (48)	125.8* (89)	80.2 (54)	106.7* (50)	55.0 (7)
	Number of illegal whitefish per lift at depth (in feet)							
	<41	41-60	61-70	71-80	81-90	91-100	101-110	>110
June.....	{ 71.4 (8)	104.7 (3)	230.0* (4)	112.2 (8)	117.7 (23)	126.7* (11)	105.0 (7)	160.0 (2)
July.....	{ 25.7 (7)	28.2 (5)	69.6 (5)	182.7* (11)	87.1 (17)	39.4 (5)	65.2* (13)	10.7 (3)
August.....	{	{ 24.0 (1)	-----	101.4* (16)	80.5 (22)	40.2 (15)	73.1* (15)	45.0 (2)
September.....	{ 4.0 (20)	21.7 (9)	20.7 (3)	23.6 (13)	35.1 (14)	70.3 (17)	111.0* (8)	-----
October.....	{ 5.5 (23)	15.9 (11)	22.7 (3)	-----	48.5* (13)	43.2 (6)	85.9* (7)	-----
Average.....	{ 16.5 (58)	29.3 (29)	93.2 (15)	100.8* (48)	79.6 (89)	67.6 (54)	83.4* (50)	63.1 (7)

deepest water (more than 110 feet). The zones of concentrations of illegal fish (seasons' average) are separated by 30 feet (difference between average depths of the intervals) as compared with 20 feet in the legal fish. This same difference is to be found in the data for the three months—June, July, and August—but is lacking in October (relatively incomplete data, however).

In general, undersized whitefish tended to live in shallower water than did legal-sized individuals. This tendency is apparent not only from the lesser depth of the inshore concentration zone (71-80 feet for illegal fish and 81-90 feet for legal fish) but also from the large numbers of small whitefish per lift in the still shallower interval, 61-70 feet. Legal-sized fish were slightly the more numerous, however, at depths shallower than 61 feet.

The vertical movements of the whitefish in northeastern Lake Michigan are the reverse of those indicated by the Lake Huron data for the Alpena-Ossineke and Saginaw Bay areas (pp. 350 and 351). In each of these regions of Lake Huron the data indicated an onshore movement of both legal and undersized fish during the summer. Whitefish of both size groups made an offshore movement in northeastern Lake Michigan.

Possible significance of two concentration zones.—The occurrence of two concentration zones of both legal and illegal whitefish in northeastern Lake Michigan³² raises the interesting question of the possible existence of distinct inshore and offshore populations or races. Certainly, the consistency of the occurrence and the seasonal move-

³² There was some indication of a similar distribution of whitefish on the Alpena-Ossineke grounds (p. 350). The data for the Saginaw Bay area (p. 351) offered only a suggestion of two concentration zones.

ments of these two concentration zones are such as to label their existence as a real phenomenon, and not a chance result to be ascribed to inadequate data. However, the mere presence of two distinct groupings of whitefish throughout all or most of the season does not make absolutely necessary the assumption of two permanently separated stocks. It is possible that conditions within the lake at certain seasons may produce an "ecological division" of an otherwise homogeneous population.

Records of a number of vertical series of temperature readings made in northeastern Lake Michigan³³ failed to give a clue to the cause of two zones of concentration of whitefish. Both the inshore and offshore concentrations of legal fish were below the thermocline³⁴ in June, July, and August and hence were in a region with extremely small temperature gradients. Preferences for water of different temperature, therefore, do not provide a logical explanation for the presence of two concentrations. The illegal whitefish of the inshore concentration were in the region of the thermocline in July and August, hence in substantially warmer water than were the fish of the offshore concentration. However, both groups were below the thermocline in June, and an inshore concentration at the thermocline was lacking in September.

Important arguments in support of the assumption of the existence of inshore and deep-water populations of whitefish are:

(1) The separation into two groups involved both large (legal) and small (illegal) fish. Consequently, the two groups are not entirely the result of different reactions of fish of different size to the same or similar environmental factors. This statement holds even though the concentration zones of the legal and illegal fish were not always identical in the same month.

(2) The fish of both concentration areas have similar seasonal vertical movements. The similarity of vertical movements kept the two zones of concentration distinct in all months but September. The presence of only one peak in the September data may represent the temporary approximation of the two concentrations or may be the result of lack of information on the distribution of whitefish beyond the 110-foot contour.

(3) There is evidence that some whitefish seldom, if ever, spawn in shallow water. The introduction of the deep trap net on gill-net grounds or in areas beyond the reach of pound nets was marked by the capture of considerable numbers of whitefish of exceptionally large size. These large fish could not be taken on these same grounds by the gill nets commonly employed since their great size prevented their becoming gilled. Pound nets, which are selective only with respect to small fish, are fully capable of taking large individuals of any size. Consequently, their failure to capture many fish as large as those found in the early catches of the deep trap nets may be taken as evidence that these giant individuals were seldom, if ever, present on the inshore pound-net grounds, at least during the period of fishing operation.

It must be remembered, nevertheless, that there is no proof that the smaller mature fish of the offshore group of whitefish do not spawn in shallow water. The separation of the whitefish into two depth groups may represent only a summer and early-autumn condition. Possibly most of the small fish of both groups spawn in shallow water and most of the large fish of both groups spawn in deeper water. However, it also seems logical to hold that the giant fish taken in deep trap nets were members of a deep-water population (that lived beyond the reach of pound nets) that had survived to a size at which they could not be taken in gill nets, and hence had become exempt from capture in the commercial fishery.

Even if the inshore and offshore groups of whitefish are held to be semi-independent or independent, it must be recognized that both groups exhibit similar fluctuations in the fishery. The records of the catch per lift and of production in M-3 (table 17 and appendix B) demonstrate a close correlation between the annual fluctuations in the

³³ Temperature data were not available from the north channel (region north of the Beaver Island archipelago), the center of the deep-trap-net fishery. However, the relatively limited local variation in temperature conditions at stations southeast, south, and northwest of Beaver Island and southeast of Manistique suggests that the data from these localities may be indicative of conditions in the area in which the deep-trap-net fishery was centered.

³⁴ The average positions of the thermocline were: last half of June, 24-33 feet; July, 67-77 feet; August, 69-80 feet; first 10 days of September, 72-86 feet. The thermocline had not yet formed in the first half of June; no readings were made in the area after September 10.

abundance of whitefish on the pound-net (shallow-water) and gill-net (deep-water) grounds of the district and also between the production of whitefish by these two gears. A similar close resemblance between the statistical data for pound nets and gill nets is to be found in other districts.

It must be remembered also that any assumption of the existence of shallow-water and deep-water stocks of whitefish in northeastern Lake Michigan does not make a similar assumption valid for any other region. In districts H-3 and H-4 of Lake Huron, for example, the simultaneous collapse of the deep-trap-net and pound-net fisheries must be interpreted as strong evidence that both gears drew a large part of their production from the same stock. It is not known, even in northeastern Lake Michigan, to what extent there may be an interchange of individuals between the inshore and offshore groups of whitefish.

SUMMARY AND COMPARISON OF THE BATHYMETRIC DISTRIBUTION OF WHITEFISH IN LAKES HURON AND MICHIGAN, WITH SPECIAL REFERENCE TO THE REGULATION OF THE FISHERY

The present study of the bathymetric distribution of the whitefish was part of a program conducted to obtain reliable data upon which to base a sound regulation of the deep-trap-net fishery. One question was: "What regulation as to the depth of water in which deep trap nets should be fished will serve best the dual purpose of protecting

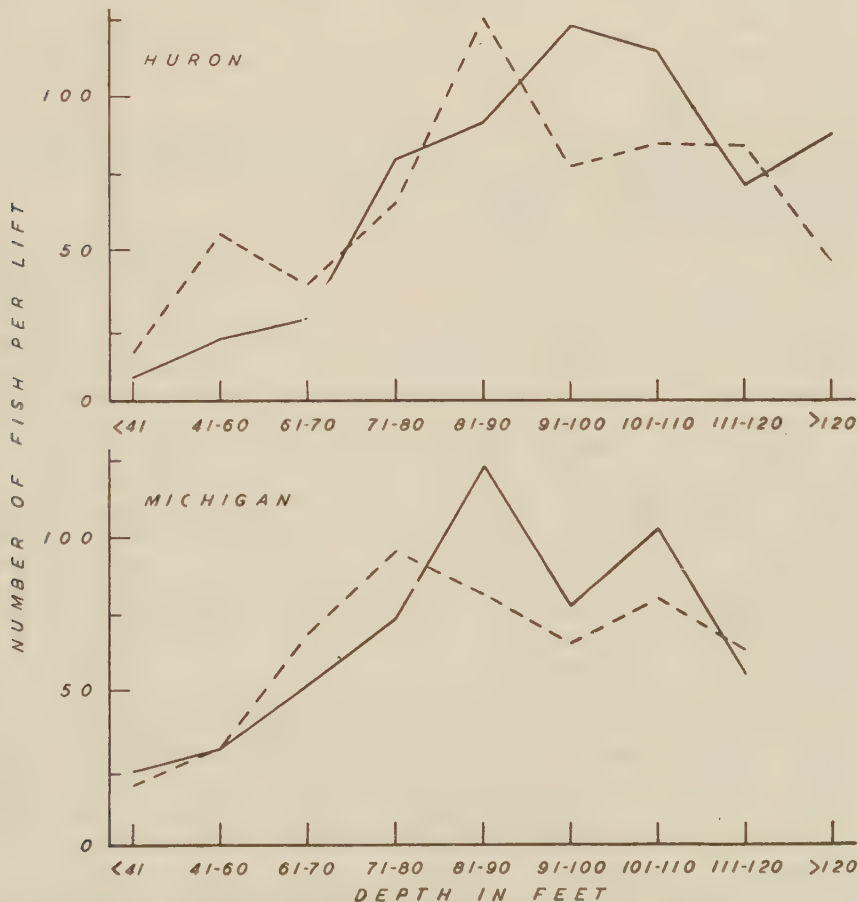


FIGURE 23.—Bathymetric distribution of legal-sized (solid lines) and illegal-sized (broken lines) whitefish in Lakes Huron and Michigan as determined from the combination of the data for all localities, years, and months in each lake.

young fish from capture and excessive handling, and of reducing production³⁵ to a level which does not threaten the extermination of the commercial stock?"

Ordinarily fishery legislation must be framed in conformity with average conditions during the entire season over a large part of a lake or an entire lake. Consequently, the most suitable data on the bathymetric distribution of whitefish in Lakes Huron and Michigan, as they pertain to fishery regulation, are those obtained by combining the available material for all grounds and all times in the fishing season in each of the two lakes. The data of table 29 (see also fig. 23) represent such combinations.

TABLE 29.—Number of legal and illegal whitefish per lift of pound nets and deep trap nets in Lakes Huron and Michigan, 1931–1932

[Number of lifts in parentheses. Asterisks indicate concentrations]

Lake	Size group	Number of whitefish per lift at depth (in feet)								
		<41	41–60	61–70	71–80	81–90	91–100	101–110	111–120	>120
Huron	Legal	7.3 (11)	20.5 (24)	26.9 (12)	79.2 (24)	91.6 (36)	123.1* (55)	114.7 (86)	70.2 (152)	87.5 (56)
	Illegal	15.9 (11)	54.9 (24)	38.2 (12)	65.3 (24)	125.8* (36)	76.9 (55)	84.2* (86)	83.7 (152)	45.7 (56)
Michigan	Legal	23.8 (64)	31.7 (38)	52.2 (21)	73.4 (51)	123.6* (91)	77.5 (56)	103.0* (52)	55.0 (7)	-----
	Illegal	19.4 (64)	31.5 (38)	68.8 (21)	95.4* (51)	81.8 (91)	65.2 (56)	80.2* (52)	63.1 (7)	-----

It should be pointed out, however, that recommendations based on the averages of table 29 which cover general conditions likewise cover very well the local conditions on the different grounds in the lake despite the variations in the bathymetric distribution of the legal and illegal whitefish in different localities.

In Lake Huron the average number of legal whitefish per lift increased continuously with increase in the depth of the water up to a maximum at 91–100 feet, decreased in the next two intervals, and increased slightly at more than 120 feet. The increase in the deepest water can be traced to the small number of lifts from this depth off Alpena, a region in which legal-sized whitefish were scarce. The limits of the general region of greatest abundance of legal fish may be set at approximately 81–110 feet. The number of undersized whitefish increased also from shallow to deeper water, but the maximum occurred at 81–90 feet, or 10 feet shallower than the depth of maximum abundance of legal fish. A second but lower peak in the number of illegal whitefish per lift was found at 101–110 feet. If legal fish are to be protected from excessive exploitation and illegal fish from frequent handling, the obvious depth limit beyond which impounding nets should not be fished in Lake Huron is 80 feet. Although this restriction curtails the production of deep trap nets severely, it cannot be considered extreme or oppressive, since a closely similar gear, the pound net, long supported a productive and prosperous fishery in even shallower water. (Few pound nets are fished in depths of more than 65 or 70 feet.)

The restriction of impounding nets in Lake Huron to depths of 80 feet or less does not mean the complete closure of the deeper waters to the commercial fishery for whitefish. These deeper areas are still open to the gill net, which was formerly the only gear fished in them. However, past experience has demonstrated that in these areas gill nets ordinarily did not catch whitefish in quantities dangerous to the stability of the stock. Furthermore, the selective action of the gill nets commonly employed precludes the capture of excessive numbers of small fish and also spares the large individuals that constitute the spawning reserve.

The Lake Michigan data differ from those of Lake Huron chiefly in the presence

³⁵ The present policy of fishery regulation in the State of Michigan waters of the Great Lakes does not include control of production through the limitation of the amount of gear fished or the setting of arbitrary limits on the season's catch.

of two distinct concentration zones for both legal and undersized fish and in showing a somewhat shallower habitat for the whitefish. The inshore concentrations, in both of which the numbers of fish per lift exceeded those of the offshore concentrations, were 10 feet shallower than the maxima for the corresponding size groups in Lake Huron. Consequently, the most suitable limit for the depth of water in which impounding nets should be operated in Lake Michigan is 70 feet, 10 feet shallower than in Lake Huron.

BATHYMETRIC DISTRIBUTION OF OTHER SPECIES

Other species were much less numerous in the catches of pound nets and deep trap nets than were whitefish. The data on the bathymetric distribution of these "miscellaneous" species, therefore, will not be given in the same detail as those on the distribution of whitefish.

LAKE TROUT

Nearly all of the lake trout (*Cristivomer namaycush*) were of legal size (minimum legal weight, 1½ pounds). As undersized lake trout were so few and because there was no evidence of important differences in the vertical distribution of legal and undersized fish, tables 30, 31, and 32 have been prepared from the records of all trout taken, regardless of size.

Lake Huron.—In the Alpena-Ossineke area (table 30) lake trout were numerous in May (31.0 to 39.8 fish per lift) at depths greater than 100 feet, but only one trout was taken in the lift from 81–90 feet. In June lake trout were fairly numerous in the shallower water (41–70 feet) while the average catch per lift declined (in comparison with the averages for May) in depths greater than 100 feet. The records for four lifts from depths between 40 and 71 feet in July and August suggest that most lake trout had abandoned the shallower water in these two months. Possibly this offshore movement accounts for the increase over the catch for the month of June in the average number of trout per lift from 81–120 feet. The average lifts in August were consistently below those of July from depths of 71–120 feet, and the September catches were smaller than those of August from the 101–120 foot interval. These decreases possibly may represent a movement of the lake trout to depths greater than those in which deep trap nets were operated.

TABLE 30.—Number of lake trout per lift of pound nets and deep trap nets in the Alpena-Ossineke area, 1931–1932

[Number of lifts in parentheses]

Month	Number of lake trout per lift at depth (in feet)							
	41–60	61–70	71–80	81–90	91–100	101–110	111–120	>120
May				{ 1.0 (1)		31.0 (1)	37.4 (23)	39.8 (4)
June	{ 21.3 (4)	40.0 (1)		12.0 (1)	8.0 (1)	16.9 (6)	11.8 (18)	18.8 (5)
July	{ 0.0 (1)		56.0 (1)	40.2 (5)	35.5 (12)	26.2 (7)	50.0 (23)	
August	{ 5.0 (2)	1.0 (1)	7.9 (7)	19.7 (9)	25.5 (3)	22.4 (5)	26.7 (10)	
September						{ 6.6 (5)	15.5 (2)	
Average	{ 13.6 (7)	20.5 (2)	13.9 (8)	24.5 (16)	31.9 (16)	19.2 (24)	33.2 (76)	28.1 (9)

The seasons' averages indicate an irregular trend toward an increase in the abundance of lake trout with increase in the depth of the water. The decline in numbers in depths of 101–110 feet may be real since similar decreases occurred in the catch for July

and August. The decline in depths greater than 120 feet may be the result of the lack of data for months later than June.

It should be emphasized that, in contrast to the whitefish data, those presented for the lake trout on the Alpena-Ossineke grounds and in other areas should not be taken as descriptive of the general distribution of trout in Lake Huron and northern Lake Michigan. The chief summer fishery for trout is conducted by gill nets at depths considerably greater than those from which the pound nets and deep trap nets were lifted. The data given here describe only the distribution of the presumably sparse inshore population of trout.

Lake trout were considerably less abundant in the Saginaw Bay area (table 31) than off Alpena and Ossineke. In four of the six months (all but July and September) the largest lifts were made from the deepest water (more than 120 feet). Trout were scarce in shallow water (less than 61 feet) in June and were not taken at all in July and August. The data fail to indicate whether the improved catches beyond 90 feet in July and August were the result of an offshore movement of an inshore group of trout or of an onshore movement of an offshore group. The averages for September and possibly October are suggestive of a migration toward deeper water.

TABLE 31.—Number of lake trout per lift of pound nets and deep trap nets in the Saginaw Bay area (ports of Au Sable-Oscoda, East Tawas, and Bay Port), 1931-1932

[Number of lifts in parentheses]

Month	Number of lake trout per lift at depth (in feet)								
	<41	41-60	61-70	71-80	81-90	91-100	101-110	111-120	>120
May						{ 1.0 (1)	2.7 (7)	3.5 (6)	3.8 (5)
June	{ 0.0 (5)	2.2 (9)	{			{ 0.0 (1)	2.4 (14)	1.8 (22)	5.0 (11)
July	{ 0.0 (6)	0.0 (1)	{		{ 5.5 (2)	7.0 (11)	10.4 (7)	5.9 (15)	5.0 (6)
August		{ 0.0 (5)	0.3 (3)	1.7 (4)	2.5 (12)	7.6 (12)	14.6 (15)	7.7 (15)	18.4 (10)
September				{ 0.5 (2)	1.0 (1)	3.0 (2)	3.0 (2)	23.2 (4)	2.5 (2)
October								{ 4.5 (2)	17.3 (3)
Average	{ 0.0 (11)	1.3 (15)	0.3 (3)	1.3 (6)	2.8 (15)	6.5 (27)	7.8 (45)	5.7 (64)	9.3 (37)

The seasons' averages show a general tendency for the number of lake trout per lift to increase with increase in the depth of water.

Tabular data are not given on the bathymetric distribution of lake trout in northern Lake Huron (Cheboygan and Rogers City area) and on the Harbor Beach grounds. (For the number of lifts at the various depths of water at these localities see tables 23 and 26.) The average number of trout per lift in northern Lake Huron varied widely (from 1.5 to 76.5 fish) with the best catch in 81-90 feet in August. Lake trout were fairly scarce on the Harbor Beach grounds. The best catches were: 20.3 fish per lift from 111-120 feet in August; 19.8 fish from depths greater than 120 feet in August; and 15.5 fish from 111-120 feet in September. Catches of lake trout were uniformly small in water shallower than 101 feet. In October only three trout were taken in a total of nine lifts, all from depths greater than 90 feet; apparently the lake trout had migrated from the Harbor Beach deep-trap-net grounds in that month.

Lake Michigan.—The rather extensive data from northeastern Lake Michigan (table 32) suggest that in certain months the lake trout as well as the whitefish may occur in two concentration zones. (See p. 353, table 28, and fig. 22.) In June and

July inshore concentrations occurred at 61–70 feet and offshore peaks at more than 110 feet. The offshore concentration in August was still in deep water but the inshore maximum was at 81–90 feet or 20 feet deeper than in June and July. (The August data were inadequate, however, for depths of less than 71 feet.) The data for September and October yield no evidence of two concentration zones of lake trout in these two months. Data were lacking, however, for depths beyond 110 feet.

TABLE 32.—Number of lake trout per lift of pound nets and deep trap nets in northeastern Lake Michigan (ports of Manistique, Epoufette, and Naubinway), 1931–1932

[Number of lifts in parentheses. Asterisks indicate concentrations]

Month	Number of lake trout per lift at depth (in feet)							
	<41	41–60	61–70	71–80	81–90	91–100	101–110	>110
June.....	{ 3.5 (8)	{ 6.3 (3)	{ 14.5* (4)	{ 10.5 (8)	{ 1.7 (23)	{ 3.1 (11)	{ 2.6 (7)	{ 5.0* (2)
July.....	{ 0.0 (7)	{ 3.6 (5)	{ 17.4* (5)	{ 10.0 (11)	{ 6.3 (17)	{ 3.4 (5)	{ 4.1 (13)	{ 17.0* (3)
August.....	{ }	{ 0.0 (1)	{ }	{ 4.2 (16)	{ 5.2* (22)	{ 2.9 (15)	{ 2.1 (15)	{ 22.5* (2)
September.....	{ 0.5 (20)	{ 0.0 (9)	{ 0.0 (3)	{ 3.1 (13)	{ 3.6* (14)	{ 1.6 (17)	{ 1.6 (8)	{ } -----
October.....	{ 0.3 (23)	{ 0.2 (11)	{ 1.3 (3)	{ } -----	{ 1.6 (13)	{ 2.2 (6)	{ 5.6* (7)	{ } -----
Average.....	{ 0.8 (58)	{ 1.3 (29)	{ 9.9* (15)	{ 6.3 (48)	{ 3.7 (89)	{ 2.5 (54)	{ 3.1 (50)	{ 15.1* (7)

There was no general agreement as to the actual location of the concentration zones of lake trout and whitefish. It is true that lake trout, large (legal) whitefish, and small (illegal) whitefish (table 28) were all concentrated at 61–70 feet in June and that both trout and legal whitefish exhibited peaks at 81–90 feet in August. On the other hand, the inshore concentration of lake trout was shallower in July than the concentration of either the legal or illegal whitefish, and the offshore concentrations of lake trout in June, July, and August were without exception deeper than the concentrations of whitefish. In October, however, a peak was evident at 101–110 feet in both lake trout and the whitefish (large and small).

Possibly it is not strictly proper to term as "concentrations" the increased abundance of lake trout at depths in excess of 110 feet, for these increases in the number per lift may be merely part of a general trend for trout to become more plentiful with increase in depth of water and not, as the term concentration implies, be indicative of a peak abundance bordered on either side by a lesser abundance.

The data of table 32 as a whole point toward an offshore movement of lake trout in northeastern Lake Michigan from June to October. (A few trout appear, however, to have returned to shallow water in October.) The seasons' averages show an increase in the catch per lift from shallow water (less than 41 feet) to a peak at 61–70 feet, followed in turn by a decline through the depth interval, 71–100 feet, and a secondary rise beyond 100 feet.

In the Green Bay region of Lake Michigan the best catches of lake trout were made in 41–60 feet in May (19.8 fish per lift). The September catches varied but little with depth of water, averaging 6.8 fish for 13 lifts in 41–80 feet and 5.0 for 4 lifts in 91–110 feet.

YELLOW PIKE

Yellow pike (*Stizostedion vitreum*) occurred in large numbers in the lifts of pound nets and deep trap nets only in the Saginaw Bay region (table 33). Because of the concentration of yellow pike in the shallower water of the area it was considered desir-

able in the preparation of the table to employ a greater number of intervals at depths less than 61 feet than was necessary in the tabulation of the data for the whitefish and the lake trout.

No data are available on the abundance of yellow pike in shallow water in May, but in June legal-sized fish (1½ pounds or larger) were plentiful in the lifts from 31–60 feet. In both May and June legal-sized yellow pike were totally lacking in all lifts from depths greater than 90 feet. The catch per lift in shallow water (less than 61 feet) declined in July and August. At the same time legal yellow pike penetrated to the greatest depths from which deep trap nets were lifted. The abundance at depths of more than 80 feet was generally higher in August than in July. Legal yellow pike were still present in the deeper water in September and October. The distribution in September was irregular. An average of 17.0 fish per lift was obtained at 111–120 feet, while yellow pike either were scarce or lacking in the lifts from other depths.

Undersized yellow pike as well as legal fish were abundant in 31–60 feet in June (with the greatest abundance in 31–40 feet) and absent from depths beyond 90 feet in both May and June. Illegal yellow pike had penetrated to a depth of 101–110 feet in July and 111–120 feet in August and September. None were taken in any month from water deeper than 120 feet.

Not only did illegal yellow pike fail to range as deep in summer as did fish of legal size, but apparently a smaller percentage of them left the shallow water. In

TABLE 33.—*Number of yellow pike per lift of pound nets and deep trap nets in the Saginaw Bay area (ports of Au Sable-Oscoda, East Tawas, and Bay Port), 1931–1932*

Month	Number of legal yellow pike per lift at depth (in feet)										
	<31	31–40	41–50	51–60	61–70	71–80	81–90	91–100	101–110	111–120	>120
May								{ 0.0 (1)	0.0 (7)	0.0 (6)	0.0 (5)
June		{ 82.6 (5)	43.7 (6)	27.0 (3)				{ 0.0 (1)	0.0 (14)	0.0 (22)	0.0 (11)
July	{ 0.3 (3)	2.0 (3)		24.0 (1)			{ 0.5 (2)	0.5 (11)	1.9 (7)	1.9 (15)	0.7 (6)
August			{ 1.0 (1)	9.2 (4)	2.5 (3)	4.5 (4)	9.7 (12)	5.8 (12)	6.4 (15)	1.7 (15)	0.4 (10)
September						{ 2.5 (2)	0.0 (1)	0.0 (2)	0.0 (2)	17.0 (4)	1.0 (2)
October										{ 1.5 (2)	0.0 (3)
Average	{ 0.3 (3)	52.4 (8)	37.6 (7)	17.7 (8)	2.5 (3)	3.8 (6)	7.8 (15)	2.8 (27)	2.0 (45)	1.9 (64)	0.3 (37)
Month	Number of illegal yellow pike per lift at depth (in feet)										
	<31	31–40	41–50	51–60	61–70	71–80	81–90	91–100	101–110	111–120	>120
May								{ 0.0 (1)	0.0 (7)	0.0 (6)	0.0 (5)
June		{ 412.8 (5)	163.0 (6)	63.7 (3)				{ 0.0 (1)	0.0 (14)	0.0 (22)	0.0 (11)
July	{ 56.0 (3)	87.7 (3)		159.0 (1)			{ 0.0 (2)	0.4 (11)	0.1 (7)	0.0 (15)	0.0 (6)
August			{ 81.0 (1)	218.0 (4)	119.5 (3)	5.0 (4)	10.0 (12)	4.7 (12)	9.5 (15)	1.9 (15)	0.0 (10)
September						{ 5.0 (2)	0.0 (1)	0.5 (2)	0.5 (2)	9.3 (4)	0.0 (2)
October										{ 0.0 (2)	0.0 (3)
Average	{ 56.0 (3)	290.9 (8)	151.3 (7)	152.8 (8)	119.5 (3)	5.0 (6)	8.0 (15)	2.3 (27)	3.2 (45)	1.0 (64)	0.0 (37)

the shallow-water lifts (less than 71 feet) the average numbers of illegal yellow pike per lift were consistently several times as great as the numbers of legal fish. Especially noteworthy were the large catches of undersized fish at these depths in July and August, months in which legal fish were scarce in shallow water. At the greater depths, however, the numbers of legal and illegal yellow pike per lift differed only slightly and in a random manner.

A total of seven yellow pike (all of legal size) was taken in northern Lake Huron (Cheboygan and Rogers City area). One of these fish was caught in 71–80 feet in July and the remaining six in 41–70 feet in September.

Yellow pike were scarce at all depths on the Alpena-Ossineke grounds, but were more numerous at depths less than 70 feet than at greater depths. No yellow pike were taken in water deeper than 90 feet before July. A few individuals (both legal and illegal) penetrated to depths of at least 111–120 feet in July and August. (No nets were lifted beyond 120 feet in these months and in September—see table 24.) In September a total of three legal fish but no illegal fish was taken from depths of 101–120 feet.

The single lift from shallow water (41–60 feet) off Harbor Beach contained eight legal and three illegal yellow pike. The maximum depths at which legal fish were taken were 111–120 feet in August and more than 120 feet in September and October. No illegal yellow pike were captured in August, but in September and October fish of this group penetrated to depths in excess of 120 feet.

Not one yellow pike was taken in the lifts of pound nets and deep trap nets in northeastern Lake Michigan. In May a total of five fish (all legal) was captured in the 10 lifts in the Green Bay area from depths of less than 61 feet and 28 yellow pike (10 legal and 18 illegal) were taken in the two lifts from 81–90 feet. No yellow pike were caught in the Green Bay area in September.

BURBOT

Because of the small total number captured and the sporadic occurrence of burbot (*Lota maculosa*) in the catches, a combination of the data for all localities appears to provide the most valid description of the inshore bathymetric distribution of the species in Lake Huron (table 34). This table cannot serve as the basis for a detailed discussion; attention will be called, however, to certain general trends. Burbot were scarce or lacking at all depths from which nets were lifted in both May and June. In June they occurred in both shallow water (less than 71 feet) and deep water (more than 100

TABLE 34.—Number of burbot per lift of pound nets and deep trap nets in Lake Huron, 1931–1932 (data for all localities combined)

[Number of lifts in parentheses]

Month	Number of burbot per lift at depth (in feet)								
	<41	41–60	61–70	71–80	81–90	91–100	101–110	111–120	>120
May.....					{ 0.0 (1)	0.0 (1)	0.2 (8)	0.5 (29)	0.2 (9)
June.....	{ 0.2 (5)	0.2 (13)	1.0 (1)		0.0 (1)	0.0 (2)	0.3 (20)	0.6 (40)	0.8 (16)
July.....	{ 0.0 (6)	0.0 (2)	0.0 (2)	0.6 (5)	2.3 (7)	3.1 (23)	0.6 (14)	0.8 (38)	0.3 (6)
August.....		{ 0.0 (7)	0.0 (4)	2.0 (13)	1.9 (23)	2.0 (17)	1.5 (22)	0.9 (29)	1.2 (15)
September.....		{ 0.0 (2)	0.8 (5)	2.6 (6)	1.2 (4)	1.3 (10)	2.2 (19)	3.2 (12)	2.8 (5)
October.....						{ 0.0 (2)	2.5 (3)	3.8 (4)	2.8 (5)
Average.....	{ 0.1 (11)	0.1 (24)	0.4 (12)	1.9 (24)	1.8 (36)	2.1 (55)	1.1 (86)	1.0 (152)	1.1 (56)

feet). Burbot were absent from shallow water in July and August, and appeared to be concentrated at intermediate depths (81–100 feet in July and 71–110 feet in August). In September and October they apparently were concentrated in depths beyond 100 feet. The changes in the average number of fish per net at the various depths for the months, July–October, suggest a general tendency for the burbot to move toward deeper water. The regular increase from July to September in the catch from 71–80 feet provides an exception to this general trend. The seasons' averages show a scarcity of burbot at depths of less than 71 feet and the greatest abundance at intermediate depths (71–100 feet), with the abundance in deep water (more than 100 feet) about half that at intermediate depths.

TABLE 35.—Number of burbot per lift of pound nets and deep trap nets in northeastern Lake Michigan (ports of Manistique, Epoufette, and Naubinway), 1931–1932

[Number of lifts in parentheses]

Month	Number of burbot per lift at depth (in feet)							
	<41	41–60	61–70	71–80	81–90	91–100	101–110	>110
June.....	{ 0.1 (8)	0.3 (3)	4.0 (4)	3.1 (8)	2.2 (23)	2.4 (11)	1.7 (7)	3.0 (2)
July.....	{ 0.0 (7)	3.2 (5)	3.0 (5)	1.6 (11)	1.9 (17)	0.8 (5)	5.4 (13)	1.3 (3)
August.....		{ 0.0 (1)		3.6 (16)	2.0 (22)	1.3 (15)	1.6 (15)	10.0 (2)
September.....	{ 0.1 (20)	1.0 (9)	4.7 (3)	2.2 (13)	3.7 (14)	2.0 (17)	2.8 (8)	
October.....	{ 1.8 (23)	4.6 (11)	10.7 (3)		8.6 (13)	2.3 (6)	5.4 (7)	
Average.....	{ 0.8 (58)	2.6 (29)	5.1 (15)	2.7 (48)	3.3 (89)	1.9 (54)	2.1 (50)	4.3 (7)

The data on the bathymetric distribution of the burbot in northeastern Lake Michigan (table 35) provide little evidence of any extensive vertical movements. Characteristic of the averages for each month appeared to be an inshore concentration at 41–60 or 61–70 feet (except in August when only one lift was observed from a depth of less than 70 feet), a reduced abundance at intermediate depths up to 101 feet (111 feet in June), and a second concentration at 101–110 feet or more than 110 feet. The average catches in October were greater than those in other months from every depth but 91–100 feet. (The average catch from 101–110 feet was the same in July and October.) The seasons' averages show an increase in the number of burbot from 0.8 in shallow water (less than 41 feet) to a maximum of 5.1 fish per lift at 61–70 feet. The average catch per net varied between 1.8 and 3.3 fish in depths of 71–110 feet and rose to 4.3 in water more than 110 feet.

WHITE SUCKER AND LONG-NOSED OR STURGEON SUCKER

Separate counts of white suckers (*Catostomus commersonnii*) and long-nosed or sturgeon suckers (*C. catostomus*) were obtained for only a limited number of lifts in the Alpena-Ossineke and Saginaw Bay areas of Lake Huron. The available data indicate that white suckers were most numerous in depths of less than 81 feet; only one individual was captured in deeper water (in 101–110 feet). Long-nosed suckers also were most plentiful inside the 81-foot contour, but were taken in fair numbers at greater depths. No long-nosed suckers were captured in depths beyond 110 feet.

PART IV OBSERVATIONS ON THE FISHING ACTION OF POUND NETS AND DEEP TRAP NETS

EFFECT OF THE SIZE OF THE MESH ON THE CATCH OF LEGAL- AND ILLEGAL-SIZED WHITEFISH AND LAKE TROUT

The question of the proper legal minimum size of mesh is a highly controversial one that involves nearly all commercial fishing gears. Certainly the most desirable size of mesh is that which releases the greatest number of illegal-sized and immature fish without serious loss of legal-sized fish. However, a great diversity of opinion exists as to what this "desirable" size of mesh may be. Although there are a few exceptions, commercial fishermen usually oppose most vigorously any attempt to increase the legal minimum mesh size, and in practice generally fish the smallest mesh permitted by law.

The lack of proper legal regulations and enforcement in the early years of the deep-trap-net fishery led to a wide range of mesh size in this gear. Many of the early deep trap nets had meshes that were ridiculously small (as small as 2¼ inches, stretched measure as fished) for a gear designed to take a species with a 2-pound legal-size limit. Continued experience, however, led many deep-trap-net fishermen to increase the size of mesh in their nets. This increase in mesh size not only reduced the labor of sorting out the illegal fish and returning them to the lake, but also improved the catch of legal fish as will now be shown.

The data in tables 36 and 37 on mesh selectivity in pound nets and deep trap nets are based on comparison of the numbers of legal- and illegal-sized whitefish (2-pound size limit) taken in nets with meshes less than 4 inches (stretched measure as fished) and in nets with meshes of 4 inches and more. For convenience in the discussion, the two groups of nets will be termed "small-mesh" and "large-mesh" nets.³⁶

Table 36 lists the total numbers of legal and illegal fish, the average numbers per lift, and the percentages of fish of both size groups in all lifts of large-mesh and small-mesh pound nets and deep trap nets observed in the course of the investigation. On the average, small-mesh nets took more fish per lift, both legal and illegal, than did large-mesh nets. The percentage of legal fish in the lift was higher (58.7 as compared with 51.3) in large-mesh nets.

TABLE 36.—*Comparison of total numbers, averages per lift, and percentages of legal and illegal whitefish taken in small-mesh and large-mesh pound nets and deep trap nets*

[The 1931-1932 data have been combined for all ports, all depths, and all months. Numbers of lifts in parentheses]

Item	Whitefish taken in mesh			
	Less than 4 inches		4 inches and more	
	Legal	Illegal	Legal	Illegal
Total number of whitefish taken.....	48,939	46,441	18,231	12,820
	(598)		(238)	
Average number of whitefish per lift.....	81.8	77.7	76.6	53.9
Corrected for equal commercial yields.....	81.8	77.7	81.8	57.6
Percentage legal and illegal.....	51.3	48.7	58.7	41.3

The unequal numbers of fish in the lifts of large-mesh and small-mesh nets make a comparison of their selective action difficult. A better comparison is made possible by the determination of the numbers of illegal fish that must be handled in nets of

³⁶ In the original compilations the nets were grouped according to mesh size by half-inch intervals. This grouping proved unsatisfactory, however, since nets that fell within some intervals of mesh size were fished chiefly on grounds with an abundance of undersized whitefish whereas the nets of other mesh sizes were fished predominantly on grounds where young whitefish were extremely scarce. In order to reduce irregularities from this source, only two size groups of mesh were employed in the preparation of data on the release of illegal-sized whitefish.

each mesh size when the commercial yields are equal. This determination (third row in body of table) shows that large-mesh nets that take an average of 81.8 legal fish may be expected to contain an average of 57.6 illegal individuals as compared with 77.7 undersized whitefish in small-mesh nets with equal commercial lifts.

From the averages of 77.7 and 57.6 illegal whitefish per lift it may be estimated that large-mesh nets released $100 \times \frac{77.7 - 57.6}{77.7}$ or 25.9 percent of the undersized individuals. For every 100 illegal whitefish taken in small-mesh nets, 74.1 should be taken by large-mesh nets with the same commercial catch.

The data of table 36 and the computations based upon them are open to the very serious objection that the actual numbers and the percentages of legal and illegal fish taken in nets of any size of mesh vary according to the nature of the stock at the place and time the nets are fished. Truly discriminating data on selectivity must be founded on the lifts of nets that are identical except for the size of mesh and that are fished under strictly comparable conditions, that is, on the same grounds, at the same depth, in the same year, and at the same time within the season.

Table 37 contains comparisons of the catch of large-mesh and small-mesh pound nets and deep trap nets, based on lifts made in the same year (1932), in the same month, on the same grounds, and at the same depth. The data are confined to comparisons in which nets of both sizes of mesh are represented by at least 5 lifts. The necessary restrictions reduced the number of possible comparisons. However, the averages of the 10 independent sets of observations are reasonably reliable.

TABLE 37.—Comparison of the numbers of legal and illegal whitefish per lift in small-mesh and large-mesh pound nets and deep trap nets fished in the same year (1932) and month, on the same grounds, and at comparable depths

[Number of lifts in parentheses]								
Fishing grounds	Month	Depth (feet)	Number of whitefish per lift in nets of mesh size				Percentage legal in nets of mesh size	
			Less than 4 inches		4 inches and more		Less than 4 inches	4 inches and more
			Legal	Illegal	Legal	Illegal		
Northeastern Lake Michigan	October	<61	16.8	4.8	22.3	2.9	77.8	88.5
	August	71-80	62.8	(6) 80.1	150.4	(22) 148.2	43.9	50.4
	June	81-90	176.0	(11) 150.1	142.5	(5) 57.1	54.0	71.4
	July	81-90	158.6	(15) 97.5	130.7	(8) 78.8	61.9	62.4
	August	81-90	121.9	(10) 64.8	233.0	(6) 108.1	65.3	68.3
	August	91-100	39.4	(14) 25.1	82.3	(8) 57.4	61.1	58.9
	September	91-100	81.5	(8) 79.3	76.8	(7) 44.0	50.7	63.6
				(6)		(8)		
Alpena-Ossineke	May	>110	41.2	288.1	24.9	154.0	12.5	13.9
	June	>110	14.2	(20) 73.2	6.0	(7) 30.6	19.0	16.4
	July	>110	26.5	(18) 54.3	49.5	(5) 97.9	32.8	33.6
				(14)		(8)		
Average			74.2	91.7	91.8	77.9	44.7	54.1
Corrected for equal commercial yields			91.8	113.4	91.8	77.9		

The averages of the 10 comparisons show that the large-mesh pound nets and deep trap nets took more legal whitefish and fewer illegal fish than the small-mesh nets fished under comparable conditions. In round numbers, small-mesh nets took an average of 92 undersized individuals in producing 74 fish of marketable size, whereas large-mesh nets took only 78 illegal whitefish for a commercial production of 92 fish. The correction for equal commercial production shows that small-mesh pound nets and deep trap nets with a commercial catch equal to that of large-mesh nets (92 fish)

may be expected to capture 113 illegal whitefish to only 78 in large-mesh nets. The release of undersized fish by large-mesh nets is, therefore, $100 \times \frac{113.4 - 77.9}{113.4}$ or 31.3 percent. This percentage of release is more reliable than the release of 25.9 percent computed from the average catches of the two groups of nets without consideration of the effects of locality, depth, and time.

That the undersized whitefish, as well as the lake trout commonly taken with them, do escape from the pots of impounding nets with the larger meshes is further suggested by the progressive increase in the average sizes of these fish with each increase in the size of mesh (table 38).

The controversy concerning the proper size of mesh in the pots of impounding nets does not, however, revolve so much around the release of undersized fish as around the escape of legal-sized fish, both whitefish and lake trout. It is not believed that any legal-sized whitefish can go through meshes smaller than $4\frac{1}{2}$ inches as found in use (the minimum size required by Michigan's law), but it is most probable that some legal-sized lake trout escape as is suggested by the larger average size of these fish in the bigger-meshed nets (table 38).

TABLE 38.—Average size of whitefish and lake trout taken from Lakes Huron and Michigan in 1931 and 1932 in impounding nets with different sizes of mesh in the pot

[Sizes of mesh represent stretched measurements as found in use. Numbers of fish employed are shown in parentheses]

Size of mesh (inches) in impounding nets	Undersized whitefish (less than 2 pounds)		Lake trout		
			Undersized (less than $1\frac{1}{2}$ pounds)	Legal-sized	
	Average total length (inches)	Average weight (lbs. and oz.)	Average weight (lbs. and oz.)	Average total length (inches)	Average weight (lbs. and oz.)
<3.....			1-4.6 (3)	18.4 (10)	2-7.2 (45)
3-3 $7/16$	{ 14.1 (54)	0-13.1 (54)		21.6 (49)	2-11.4 (90)
3 $1/2$ -3 $15/16$	{ 17.6 (123)	1-9.6 (123)	1-5.2 (18)	22.1 (189)	2-11.2 (395)
4-4 $7/16$	{ 17.8 (36)	1-10.2 (36)	1-5.4 (4)	23.5 (20)	2-14.9 (203)
4 $1/2$ -4 $15/16$					{ 3-8.6 (7)

Additional information on this question of escapement is provided by the length and weight frequencies of the whitefish and lake trout gilled in the different sizes of mesh (tables 39, 40, 41, and 42). Table 39 shows that all of the whitefish gilled in meshes smaller than 3 inches were undersized. Presumably, then, no legal-sized whitefish can escape through these meshes. It was not until a mesh of $3\frac{1}{2}$ to 3 $15/16$ inches (about 4 to 4 $7/16$ inches as manufactured) was used that legal-sized whitefish were gilled in any numbers, although 91 percent of the gilled fish were still below the 2-pound legal limit. Even the largest meshes for which data are adequate (4 to 4 $7/16$ inches) did not permit many of the smaller fish to escape as 79 percent of the gilled individuals in these meshes were undersized, and the average weight of all fish was noticeably less than 2 pounds (1 pound, 11 ounces).

It is of interest to note from the frequencies that the bulk of the gilled whitefish varied from 1 to 2 pounds in weight in meshes of 3 to 3 $15/16$ inches and from 1 to $2\frac{1}{4}$ pounds in the larger meshes—a range of only 1 or $1\frac{1}{4}$ pounds. The corresponding range in length of these fish (table 40) was $3\frac{1}{2}$ inches ($15 - 18\frac{1}{2}$; $15\frac{1}{2} - 19$; $16 - 19\frac{1}{2}$ inches).

The progressive increase in the average weight of the undersized gilled whitefish, as well as in the average length (table 40), with each increase in the size of mesh

indicates that some of the smallest individuals escaped. The average weight of the legal-sized, gilled whitefish, however, did not increase progressively with an increase in mesh size (the average length showed a slight increase), thus suggesting that virtually no whitefish of 2 pounds or larger passed through any of the meshes for which there were adequate data.

TABLE 39.—Weight frequencies and average weights of whitefish gilled in the pots of impounding nets of Lakes Huron and Michigan, 1931-1932

[The weight intervals apply to fish with weights up to but not including the upper limit. Undersized fish were separated on the basis of a 2-pound limit]

Weight interval (pounds)	Sizes of stretched mesh (inches) as found in use					Total number
	<3	3-3 7/16	3 1/2-3 15/16	4-4 7/16	4 1/2-4 15/16	
1/4 to 1/2	2	1	1			4
1/2 to 3/4	7	7	4			18
3/4 to 1	2	5	9	6		22
1 to 1 1/4	3	24	75	29		131
1 1/4 to 1 1/2	1	23	118	45		187
1 1/2 to 1 3/4		27	114	50		191
1 3/4 to 2	2	16	63	35		116
2 to 2 1/4		2	20	24		46
2 1/4 to 2 1/2		1	14	10	1	26
2 1/2 to 2 3/4		1	3	4		8
2 3/4 to 3				4		4
3 to 3 1/4			1	2		3
5 to 5 1/4				1		1
Total	17	107	422	210	1	757
Number of undersized fish	17	103	384	165	0	669
Number of legal-sized fish	0	4	38	45	1	88
Percentage of undersized fish	100.0	96.3	91.0	78.6	0.0	88.4
Average weight of all fish	0-14.4	1-6.1	1-8.0	1-11.0	2-4.0	1-8.4
Average weight of undersized fish	0-14.4	1-5.5	1-6.9	1-7.7		1-6.6
Average weight of legal-sized fish		2-5.1	2-3.8	2-5.6	2-4.0	2-4.8

TABLE 40.—Length frequencies and average lengths of whitefish gilled in the pots of impounding nets of Lakes Huron and Michigan, 1931-1932

[The total-length intervals apply to fish with lengths up to but not including the upper limit. The average lengths of legal-sized and undersized fish were based only on those individuals for which records of weight also were available (number of specimens in parentheses). Undersized fish were separated on the basis of a 2-pound limit, not on length]

Total length interval (inches)	Sizes of stretched mesh (inches) as found in use					Total number
	<3	3-3 7/16	3 1/2-3 15/16	4-4 7/16	4 1/2-4 15/16	
11 1/2 to 12	1		1			2
12 to 12 1/2		1				1
12 1/2 to 13	2					2
13 to 13 1/2	5	1	4			10
13 1/2 to 14		6	1	1		8
14 to 14 1/2	1	2	2	2		7
14 1/2 to 15	1	5	3	5		14
15 to 15 1/2	1	12	13	6		32
15 1/2 to 16		12	45	9		66
16 to 16 1/2	2	14	58	19		93
16 1/2 to 17	2	10	65	25		102
17 to 17 1/2	1	12	86	32		131
17 1/2 to 18		14	53	20		87
18 to 18 1/2	2	15	40	27		84
18 1/2 to 19		6	22	27		55
19 to 19 1/2		5	15	18	1	39
19 1/2 to 20			7	5		12
20 to 20 1/2			6	9		15
20 1/2 to 21			1	3		4
21 to 21 1/2			1	2		3
24 to 24 1/2				1		1
Total	18	115	423	211	1	768
Average total length (inches) of all fish	14.7	16.5	17.0	17.6	19.2	17.0
Average total length (inches) of undersized fish	14.5 (17)	16.5 (103)	16.7 (356)	17.0 (160)		16.7 (636)
Average total length (inches) of legal-sized fish		18.9 (4)	19.1 (36)	19.4 (43)	19.2 (1)	19.2 (84)

TABLE 41.—*Weight frequencies and average weights of lake trout gilled in the pots of impounding nets of Lakes Huron and Michigan, 1931-1932*

[The weight intervals apply to fish with weights up to but not including the upper limit.
Undersized fish were separated on the basis of a 1½-pound limit]

Weight interval (pounds)	Sizes of stretched mesh (inches) as found in use				Total number
	<3	3-3 7/16	3 1/2-3 15/16	4-4 7/16	
1 to 1 1/4.....	3	2	6		11
1 1/4 to 1 1/2.....	1	5	12		18
1 1/2 to 1 3/4.....		9	39	2	50
1 3/4 to 2.....		6	38	5	47
2 to 2 1/4.....		3	34	5	42
2 1/4 to 2 1/2.....		1	21	8	30
2 1/2 to 2 3/4.....		2	4	1	7
2 3/4 to 3.....		1	4	1	6
3 to 3 1/4.....				2	2
3 1/4 to 3 1/2.....			1		1
3 3/4 to 4.....			1	1	2
Total.....	4	29	158	25	216
Number of undersized fish.....	4	7	18	0	29
Number of legal-sized fish.....	0	22	140	25	187
Percentage of undersized fish.....	100.0	24.1	11.4	0.0	13.4
Average weight of all fish.....	1-2.8	1-11.8	1-14.4	2-4.6	1-14.6
Average weight of undersized fish.....	1-2.8	1-4.9	1-5.0		1-4.7
Average weight of legal-sized fish.....		1-14.0	1-15.6	2-4.6	2-0.8

TABLE 42.—*Length frequencies and average lengths of lake trout gilled in the pots of impounding nets of Lakes Huron and Michigan, 1931-1932*

[The total-length intervals apply to fish with lengths up to but not including the upper limit. The average lengths of legal-sized and undersized fish were based only on those individuals for which records of weight also were available (number of specimens in parentheses). Undersized fish were separated on the basis of a 1½-pound limit, not on length]

Total length interval (inches)	Sizes of stretched mesh (inches) as found in use				Total number
	<3	3-3 7/16	3 1/2-3 15/16	4-4 7/16	
15 1/2 to 16.....			1		1
16 to 16 1/2.....	2	1			3
16 1/2 to 17.....		1	4		5
17 to 17 1/2.....	3	1	13		17
17 1/2 to 18.....		2	21		23
18 to 18 1/2.....		6	27		33
18 1/2 to 19.....		3	30		33
19 to 19 1/2.....		7	28	3	38
19 1/2 to 20.....		1	22	1	24
20 to 20 1/2.....		4	13	8	25
20 1/2 to 21.....			13	5	18
21 to 21 1/2.....		2	19	3	24
21 1/2 to 22.....		1	6	2	9
22 to 22 1/2.....			2	2	4
22 1/2 to 23.....			5		5
23 to 23 1/2.....				1	1
23 1/2 to 24.....			1		1
24 to 24 1/2.....				1	1
Total.....	5	29	205	26	265
Average total length (inches) of all fish.....	16.8	18.8	19.1	20.7	19.2
Average total length (inches) of under- sized fish.....	16.9 (4)	17.3 (7)	17.2 (18)		17.2 (29)
Average total length (inches) of legal- sized fish.....		19.3 (22)	19.4 (136)	20.6 (24)	19.5 (182)

The situation with respect to the lake trout was somewhat different. The few trout gilled in meshes smaller than 3 inches were all undersized (less than 1½ pounds) (table 41). The legal-sized trout started to gill noticeably in meshes of 3 to 3 7/16 inches. Only 24 percent of the gilled fish in these meshes were undersized, and the average weight (1 pound, 11.8 ounces) of all gilled fish was well over the legal size limit. The percentage of undersized gilled trout decreased to 11.4 in the 3½- to 3 15/16-inch meshes, and no illegal-sized fish were gilled in larger meshes. An exam-

ination of the frequencies and averages indicates that probably few legal-sized trout escaped through the meshes of $3\frac{1}{2}$ to $3\frac{15}{16}$ inches (about 4 to $4\frac{7}{16}$ inches as manufactured) since the modal weight of the fish in these meshes (between $1\frac{1}{2}$ and $1\frac{3}{4}$ pounds) was the same as in the 3- to $3\frac{7}{16}$ -inch meshes and the average weight of legal-sized fish increased only 1.6 ounces in nets of the latter sizes of mesh. Individuals of these sizes did escape through meshes larger than $3\frac{15}{16}$ inches. It is doubtful, however, whether many fish of $1\frac{3}{4}$ pounds or larger were able to pass through meshes of exactly 4 inches (about $4\frac{1}{2}$ inches as manufactured).

It may be observed from the frequencies of weights that the bulk of the gilled trout shifted to a higher weight-interval with each increase in the mesh between 3 and $4\frac{7}{16}$ inches, but the fish were always concentrated within a relatively small range of weight ($\frac{3}{4}$ to 1 pound). The majority of the gilled trout weighed between $1\frac{1}{4}$ and 2 pounds in the 3- to $3\frac{7}{16}$ -inch mesh, between $1\frac{1}{2}$ and $2\frac{1}{2}$ pounds in the $3\frac{1}{2}$ - to $3\frac{15}{16}$ -inch mesh, and between $1\frac{3}{4}$ and $2\frac{1}{2}$ pounds in the 4- to $4\frac{7}{16}$ -inch mesh. The ranges in length of the bulk of the trout (table 42) varied from about 1 to $2\frac{1}{2}$ inches in these various meshes (18 - $19\frac{1}{2}$; $17\frac{1}{2}$ - 20; 20 - 21 inches).

The average weight of the undersized gilled trout, as well as the average length (table 42), increased with an increase in the size of mesh from less than 3 inches to 3 to $3\frac{7}{16}$ inches (indicating release of some small fish). The size of fish did not change, however (slight increase in weight; slight decrease in length), with a further increase of $\frac{1}{2}$ inch in mesh size suggesting that, though additional undersized fish were released by the larger meshes, the size of mesh was not yet sufficiently large to permit the larger undersized trout to escape. An increase of another $\frac{1}{2}$ inch in the size of the mesh apparently did permit this escapement for no undersized trout were gilled in meshes of 4 to $4\frac{7}{16}$ inches. Even though these meshes or larger ones are used, it may not be assumed that no undersized fish would remain in the net. They do not all attempt to escape.

The average weight and length of the legal-sized gilled trout increased slightly with an increase in mesh size from 3 to $3\frac{7}{16}$ to $3\frac{1}{2}$ to $3\frac{15}{16}$ inches (indicating release of only a few fish), but increased to a greater degree with a further $\frac{1}{2}$ -inch increase of mesh size, suggesting that some of the smaller fish of legal size had escaped. Nearly all of the trout gilled in meshes of 4 to $4\frac{7}{16}$ inches weighed $1\frac{3}{4}$ pounds or more.

In general, the data on the gilled fish and on the average sizes of fish retained in the impounding nets indicate that Michigan's minimum size of mesh ($4\frac{1}{2}$ inches as found in use) prescribed for the pots of impounding nets employed in catching whitefish and lake trout should not be reduced. This mesh is in fact too small to liberate a large proportion of the undersized whitefish found in the nets, although on the other hand it is too large to hold the smaller individuals of the legal-sized trout. A 4-inch mesh as found in use would probably prove more effective for the capture of trout at the present size limit of $1\frac{1}{2}$ pounds. A better solution than a reduction in mesh to prevent the escape of legal-sized trout would be a substantial increase in the legal size limit since most lake trout (especially the females) under 3 pounds are sexually immature. It is not practicable to prescribe different meshes for whitefish and trout as both species are usually taken together on the same grounds. Further, a $4\frac{1}{2}$ -inch mesh is also prescribed for gill nets employed for both species.

DESTRUCTION OF WHITEFISH THROUGH GILLING IN THE MESHES OF POUND NETS AND DEEP TRAP NETS

The gilling of undersized fish in the meshes of impounding nets constitutes a certain source of destruction since death follows soon after the individual is enmeshed. It is, therefore, of importance to know what percentage of the illegal-sized whitefish become gilled in commercial pound nets and deep trap nets, and how this percentage varies with the size of the mesh. The death of legal individuals through gilling is of lesser importance, although the market value of such fish may be impaired and large numbers of gilled fish of any size add considerably to the fishermen's labor in clearing their nets.

The data of table 43 on the numbers and percentages of gilled whitefish in pound nets and deep trap nets are based on a combination of all nets of similar sizes of mesh irrespective of fishing grounds, depth of water, and the month and year in which the nets were fished.³⁷ None of these variables was found to affect the percentage of gilled fish.

TABLE 43.—Numbers and percentages of legal and illegal whitefish gilled in large-mesh and small-mesh pound nets and deep trap nets, 1931–1932 data combined for all localities and all depths of water

[The table is based only on the lifts in which gilled fish were counted and separated according to size]

Item	Whitefish taken in nets of mesh size			
	Less than 4 inches		4 inches and more	
	Legal	Illegal	Legal	Illegal
Total number of whitefish taken.....	48,441	44,759	18,024	12,613
Number of whitefish gilled.....	154	1,077	161	340
Percentage of gilled whitefish.....	0.3	2.4	0.9	2.7

A larger percentage of both the legal and the illegal whitefish became gilled in large-mesh nets than in small-mesh nets. The percentage of the legal fish gilled in large-mesh nets although small was three times that gilled in small-mesh nets, but the percentage of the illegal fish gilled in large meshes was only slightly above that in small meshes. It may be considered probable that the greater ability of large meshes to gill the larger illegal fish is compensated by the numbers of smaller illegal fish that can pass through the meshes.

The percentages of gilled illegal whitefish in pound nets and deep trap nets (2.4 percent in small meshes and 2.7 percent in large meshes) do not point to gilling as a very important source of destruction of undersized fish in a single lift. Should the same fish be taken repeatedly the risk of death by gilling would be increased.

BLOATING OF LIVE WHITEFISH IN POUND NETS AND DEEP TRAP NETS

Another possible source of destruction of illegal-sized whitefish is the bloating (the result of changing pressure) that frequently occurs when nets are lifted. It cannot be stated exactly how serious the effects of bloating may be. It is possible that many fish that are not visibly bloated when a net reaches the surface may have been injured seriously by the change of pressure, particularly if the net was lifted rapidly. On the other hand, visibly bloated fish often appear to make a complete recovery, and swim away vigorously upon return to the water.

Table 44 shows the relationship between the depth of water from which nets were lifted and the extent of bloating of whitefish of legal and illegal size. The percentage

TABLE 44.—Relationship between the depth of water and the bloating of live whitefish in pound nets and deep trap nets, 1931–1932 data combined for all localities

Depth of water (feet)	Total number of fish ¹	Number of bloated fish	Percentage bloated fish	Percentage bloated legal fish ²	Percentage bloated illegal fish ²
<61.....	7,206	0	0.00	0.00	0.00
61 to 80.....	14,811	66	0.45	0.46	0.44
81 to 100.....	45,109	223	0.49	0.31	0.72
101 to 110.....	24,493	265	1.08	0.65	1.66
>110.....	31,029	527	1.70	1.33	2.08
Total or average.....	122,648	1,081	0.88	0.63	1.17

¹ Includes only lifts in which bloated fish were counted.

² Only 63 percent of the bloated fish were separated as to size.

³⁷ Fish were considered to be gilled only when it was obvious that they had become enmeshed while the net was actually fishing. Freshly gilled live fish were considered to have become enmeshed during the lifting process, and were not counted; usually they were not injured.

of bloated fish (legal and illegal fish combined) in the lift rose consistently as the depth of water increased. No fish were bloated in nets (mostly pound nets) set at depths of 60 feet and less. At depths of 61–80 and 81–100 feet slightly less than one-half of one percent were bloated. The percentage of bloated whitefish increased to 1.08 in 101–110 feet, and rose still further to 1.70 percent in deep water (more than 110 feet).

The data on the percentages of the legal and of the illegal whitefish that were bloated reveal that both sizes of fish share the general trend toward increased bloating with increase in the depth of the water. The greater percentage of bloated legal fish at 61–80 feet in comparison with the percentage at 81–100 feet constitutes the only exception. At all depths beyond 80 feet relatively more of the illegal whitefish than of the legal whitefish were bloated. This difference was probably due to the thinner body wall of the younger fish. The averages for fish taken at all depths show that 0.63 percent of all legal fish and 1.17 percent of all illegal fish were bloated.

The bloating of live whitefish was probably an unimportant source of destruction of undersized individuals. Only 1.17 percent of all illegal fish were bloated and the maximum percentage of bloated fish at any one depth was 2.08 (deep water). However, the repeated capture of undersized fish would increase the risk of injury or death through bloating.

DEAD WHITEFISH IN POUND NETS AND DEEP TRAP NETS

Commercial fishermen opposed to the use of deep trap nets contended that confinement in this type of gear was fatal to whitefish and that dead illegal fish were very numerous in the lifts. The data of table 45, which show the number and percentage of dead fish (exclusive of dead gilled fish) at three different depths and the percentages of the legal and of the illegal fish found dead at these same depths, do not, in general, support this contention.

TABLE 45.—*Relationship between the depth of the water and the numbers and percentages of dead whitefish in deep trap nets in Lakes Huron and Michigan, 1931–1932 data combined for all localities in each lake*

Lake	Depth of water (feet)	Total number of fish ¹	Number of dead fish	Percentage dead fish	Percentage dead legal fish ²	Percentage dead illegal fish ²
Huron	<81	4,734	107	2.26	0.44	3.96
	81 to 110	35,736	209	0.58	0.32	0.90
	>110	30,313	195	0.64	0.45	0.84
	All depths	70,783	511	0.72	0.38	1.10
Michigan	<81	11,613	24	0.21	0.05	0.35
	81 to 110	36,215	69	0.19	0.08	0.35
	>110	827	2	0.24	0.26	0.22
	All depths	48,655	95	0.20	0.08	0.35

¹ Includes only lifts in which dead fish were counted.

² Only 72 percent of the dead fish were separated as to size.

Almost 4 percent of the undersized whitefish were dead in the Lake Huron deep trap nets lifted from depths of 80 feet or less. However, at that time (1931–1932) relatively few deep trap nets were fished in such shallow water. Less than 1 percent of the illegal whitefish were dead in nets lifted from greater depths. The average percentage of the undersized fish found dead in the lifts of all deep trap nets observed in Lake Huron was slightly above 1 percent. The percentage of the dead among the legal whitefish in Lake Huron deep trap nets was small (average, 0.38 percent) and showed little variation with the depth of the water.

The percentages of both the legal and the illegal whitefish found dead in deep trap nets were much smaller in Lake Michigan than in Lake Huron. The shallow-water lifts (80 feet and less) in particular had relatively few dead fish as compared with nets from the same depth in Lake Huron. The percentages of dead whitefish in Lake

Michigan do not appear to vary according to the depth of the water. (The data for deep-water lifts are too scanty to be reliable.)

Although it cannot be said that deep-trap-net lifts contained large numbers of dead whitefish, there is good evidence that pound-net lifts contained even fewer. Not one dead whitefish was found in all the pound-net lifts observed in Lake Michigan. In Lake Huron pound nets only 0.61 percent of the whitefish were dead (0.94 percent of the legal fish and 0.45 percent of the illegal fish). The percentage of dead legal fish was rather high, but the percentage of dead undersized fish was far below that for deep trap nets in shallow water (80 feet and less).

ESTIMATES OF THE PROBABLE DESTRUCTION OF ILLEGAL-SIZED WHITEFISH IN CERTAIN LOCALITIES AND YEARS

It may be stated that the percentage of undersized whitefish handled by the fishermen and destroyed in the lifting of pound nets and deep trap nets was small, although that percentage was somewhat larger for deep trap nets than for pound nets. If we define as "known destruction" the quantities of whitefish dead at the time the nets were lifted (including dead gilled fish), the data of the preceding sections make possible the following estimates of the percentages of the undersized whitefish destroyed in Lakes Huron and Michigan in pound nets and deep trap nets of different sizes of mesh:

Lake	Mesh size	Pound nets	Deep trap nets
Huron	Less than 4 inches	2.85	3.50
	4 inches and more	3.15	3.80
Michigan	Less than 4 inches	2.40	2.75
	4 inches and more	2.70	3.05

These estimates, percentages of "known destruction," range from 2.40 to 3.80. To the "known" destruction of undersized whitefish must be added the undetermined loss that resulted from the death of bloated live fish (this loss could not have been much greater than 1 percent—see table 44) and of fish killed or injured fatally during the sorting of the catch.

Despite the fact that the percentage of the undersized whitefish that was destroyed in a single lift was relatively small, the total destruction during the entire season may have been considerable, especially in those localities where the fishery was intensive and young whitefish were abundant. It is of some interest, therefore, to have estimates of the total number of undersized whitefish captured by pound nets and deep trap nets and of the total "known" destruction in certain fishing areas (table 46).

The estimates of the total number of young whitefish captured were based on the known number of nets lifted (as determined from fishermen's reports) and the average

TABLE 46.—*Estimated numbers of illegal-sized whitefish captured by pound nets and deep trap nets in certain areas of Lakes Huron and Michigan in certain calendar years, and the estimated known destruction (fish dead at time of lifting) of undersized whitefish*

Statistical districts	Year	Undersized fish taken			Known destruction		
		Pound nets	Deep trap nets	Both	Pound nets	Deep trap nets	Both
H-2	{ 1931	127,000	321,000	448,000	3,600	11,400	15,000
	{ 1932	64,000	180,000	244,000	1,900	6,400	8,300
H-3, H-4	{ 1931	198,000	124,000	322,000	5,600	4,400	10,000
	{ 1932	113,000	269,000	382,000	3,200	9,600	12,800
H-5	{ 1932		130,000	130,000		4,600	4,600
	{ 1933		616,000	616,000		21,700	21,700
M-2, M-3	{ 1931	136,000	169,000	305,000	3,600	4,800	8,400
	{ 1932	120,000	315,000	435,000	3,200	8,900	12,100

number of undersized whitefish per lift (as determined from our observations in the field). Estimates were made separately for large-mesh (4 inches and greater) and small-mesh (less than 4 inches) nets and combined to obtain the totals listed in the table. It was necessarily assumed that the relative numbers of large-mesh and small-mesh nets in the general fishery were the same as those observed by our investigators in the field. Estimates were made of the capture and destruction of illegal-sized whitefish by deep trap nets in H-5 in both 1932 and 1933, although field observations³⁸ were made only in 1932. The computations for 1933 (based on the assumption that the abundance of young whitefish and the relative numbers of large-mesh and small-mesh nets were the same in that year as in 1932) were carried out merely to provide a rough idea of the large numbers of whitefish that probably were handled during the years of intensive fishing in southern Lake Huron.

The estimated numbers of young whitefish handled by pound-net and deep-trap-net fishermen in the various districts and years were large (130,000 to 616,000). The estimated destruction, however, appeared to be relatively small (4,600 to 21,700). The combination of the data for all districts and years indicates a loss of 2.8 percent of all undersized whitefish taken in pound nets and of 3.4 percent of those captured by deep trap nets. These figures should not be taken as indicative of the percentage loss of the total population of undersized fish (of the sizes handled) as many fish may have been captured more than once and others, doubtless, were not captured at all.

Estimates were made also of the loss of small whitefish in the entire lakes (Michigan waters) in 1932, the year of our most extensive field observations. The 1932 pound-net yield in districts H-2 to H-5, inclusive, amounted to 43.5 percent of the catch of whitefish in pound nets in the entire lake. The "known" destruction of whitefish by pound nets in these districts in 1932 amounted to 5,100 individuals (table 46). If the average conditions of the pound-net fishery (abundance of young fish on the grounds and relative numbers of large-mesh and small-mesh nets) in H-1 and H-6 are assumed to have been similar to those of the fishery in H-2 to H-5, the "known" destruction of undersized whitefish in the pound nets of all Michigan waters of Lake Huron in 1932 can be calculated as $5,100/0.435$ or 11,700 fish. Similarly, the deep trap nets of districts H-2 to H-5 accounted for 93.8 percent of the total deep-trap-net catch and for the estimated destruction of 20,600 young whitefish. The estimated "known" destruction for all six districts was, therefore, $20,600/0.938$ or 22,000 fish. The combined "known" destruction of pound nets and deep trap nets in Lake Huron in 1932 was 33,700 whitefish.

The same calculations for the Michigan waters of Lake Michigan showed that in 1932 districts M-2 and M-3 yielded 52.1 percent of the total catch of whitefish in pound nets and 76.5 percent of the deep-trap-net production. These percentages applied to the figures on "known" destruction in table 46 yielded the following estimates of the loss of undersized whitefish in all eight districts: pound nets—6,100; deep trap nets—11,600; pound nets and deep trap nets—17,700.

The estimates of the "known" destruction of undersized whitefish by deep trap nets in all Michigan waters of Lakes Huron and Michigan in 1932 (22,000 and 11,600 individuals, respectively) can not be termed large. If that gear was extremely harmful to the stocks of small fish the loss must have occurred through the death of fish that were killed or injured fatally in the sorting of the catch.

The opinions of the fishermen concerning the ability of the whitefish to withstand handling were found to vary widely. Some (particularly those who were opposed to the use of deep trap nets) contended that whitefish are extremely delicate—that they are unable to survive removal from the water for even short periods of time and will die as the result of the least amount of handling. Others (especially deep-trap-net fishermen) held that the whitefish is exceptionally hardy—that with only reasonable care very few or none at all are injured during the sorting of the catch.

Data are not available to show which of the above diametrically opposite viewpoints is the more nearly correct. However, the fact that 101 or 22.1 percent of 457

³⁸ The pound-net fishery for whitefish was negligible in H-5 in 1932 and 1933 (appendix B). Our investigators observed no pound-net lifts in this district.

young whitefish tagged in Lake Michigan were later recovered (Smith and Van Oosten, 1940)³⁹ suggests that they successfully withstand careful handling.

Our field investigators reported that almost all deep-trap-net fishermen were extremely careful in the sorting of the catch. To be sure, they may have been more than ordinarily painstaking when the investigators were aboard their craft. Nevertheless, most of them appeared to be following a well established routine that involved a minimum of handling of illegal-sized whitefish and a minimum length of time out of the water. Only one fisherman was observed whose method of sorting was considered likely to result in the death of a high percentage of the undersized whitefish.

The fact that the illegal whitefish taken by the deep trap nets in Lakes Huron and Michigan were so near the legal size increased greatly the potential harm resulting from the destruction of undersized individuals. It was estimated that practically all of the illegal-sized whitefish observed would have attained the legal weight of 2 pounds within another year, as their average weight at capture was 1 pound, 9.7 ounces (17.6 inches, total length). However, the illegal-sized whitefish from the pound nets of Lake Huron (no data from Lake Michigan pound nets) were relatively small (13.1 ounces and 14.1 inches, total length).

SHRINKAGE OF THE TWINE IN POUND NETS AND DEEP TRAP NETS

The fact that pound-net and deep-trap-net twine is treated regularly (usually in the spring of each year) with tar or copper oleate as a preservative gives rise to a troublesome question as to whether the minimum legal size of the mesh shall be designated "as found in use" or "as manufactured." It is well known that the application of a net preservative to cotton twine is almost always accompanied by some shrinkage. However, the exact extent of this shrinkage is not predictable for individual nets. The amount of shrinkage of the twine varies with the method of applying the treatment, the number of times the webbing is treated, the nature of the webbing as received from the manufacturer, and possibly with the type of preservative employed. If the minimum legal mesh size is defined "as found in use," honest fishermen conceivably might find themselves confronted with the problem of large amounts of expensive gear rendered useless by unexpected high shrinkage. On the other hand, if the minimum mesh size is defined "as manufactured," unscrupulous fishermen may so control the type of twine purchased and the method of preservation as to shrink the mesh to a size far below the intended legal minimum. Regardless of how the legal minimum mesh size is designated, it is of importance to have data available on the average amount and the range of the shrinkage of pound-net and deep-trap-net twine following the application of a preservative.

The results of 648 measurements of pound-net and deep-trap-net meshes as found in use are recorded in table 47.⁴⁰ The data have been grouped according to the size of the mesh (extension measure) as manufactured and to the type of preservative applied. The former grouping (as to size of mesh when manufactured) is based entirely on the fishermen's statements. The meshes were measured by inserting a thin steel rule in one end of the collapsed mesh, pulling the twine taut, and reading the length between and inside the knots (not from the centers of the knots). Measurements were made both parallel with the selvage (first measurement of each series in table 47) and at right angles to it (second measurement).

Although most of the fishermen who were interviewed believed that tar shrinks webbing more than does copper oleate, their belief is not entirely supported by the data of table 47. It is true that tarred nets of 4¼-inch and 4½-inch original mesh size suffered greater shrinkage than nets of the same mesh size treated with copper oleate. On the other hand, nets with a factory measurement of 3½ inches shrank considerably more under copper-oleate treatment than did nets of the same mesh size treated with tar; a slightly greater shrinkage from copper oleate was found also for 4-inch-mesh nets. If all sizes of mesh are considered together, there appears to be little difference between the

³⁹ Smith, Oliver H. and John Van Oosten. Tagging Experiments with Lake Trout, Whitefish, and Other Species of Fish from Lake Michigan. *Trans. Am. Fish. Soc.*, vol. 69, (1939) 1940, pp. 63-84.

⁴⁰ The data of table 47 do not represent 648 different nets as some nets were visited more than once. Several nets of mesh size larger than 4½ inches as manufactured were measured, but there were not enough of any single mesh size to yield reliable averages.

TABLE 47.—*Shrinkage of pound-net and deep-trap-net twine following the application of tar or copper oleate as preservatives*

[The average amounts of shrinkage are given in parentheses below the average measurements of the meshes as found in use. All averages are to the nearest sixteenth of an inch]

Type of treatment	Size of mesh as manufactured							
	3 1/2 inches		4 inches		4 1/4 inches		4 1/2 inches	
	Number of measurements	Mesh size as fished	Number of measurements	Mesh size as fished	Number of measurements	Mesh size as fished	Number of measurements	Mesh size as fished
Tar.....	38	{ 3 1/8x3 1/8 (6/16x6/16) }	144	{ 3 9/16x3 5/8 (7/16x6/16) }	59	{ 3 13/16x3 15/16 (7/16x5/16) }	206	{ 3 7/8x3 15/16 (10/16x9/16) }
Copper oleate.....	47	{ 2 15/16x3 (9/16x8/16) }	80	{ 3 9/16x3 9/16 (7/16x7/16) }	34	{ 3 15/16x4 (5/16x4/16) }	40	{ 4 1/16x4 1/8 (7/16x6/16) }
Total or average.....	85	{ 3x3 1/16 (8/16x7/16) }	224	{ 3 9/16x3 5/8 (7/16x6/16) }	93	{ 3 7/8x4 (6/16x5/16) }	246	{ 4x4 (9/16x8/16) }

shrinkage produced by tar and by copper oleate. With both treatments measurements made parallel with the selvage showed on the average 1/16 inch greater shrinkage than did those made at right angles to the selvage.

The data for individual nets showed a variation from "no shrinkage" to a maximum shrinkage of 1 inch. It is this wide range of variation in shrinkage that makes the designation of the legal minimum mesh in terms of "size as manufactured" so eminently undesirable. The average shrinkage of meshes measured in this study was 7/16 inch or slightly less than 1/2 inch. If it were known that the shrinkage of all nets closely approximated this average, the designation of a legal minimum mesh size (as manufactured) 1/2 inch larger than that intended for nets as found in use might prove reasonably satisfactory. However, the wide range of shrinkage makes such a procedure impractical. If the legal minimum mesh is to be defined "as manufactured," allowance should be made not for the average observed shrinkage but for the maximum possible shrinkage. A further objection to the designation of the legal minimum mesh size "as manufactured" lies in the fact that illegal nets can be fished with impunity if they have been treated before examination by a conservation officer. In other words, there is no exact means of determining the original mesh size of a treated net.

The conclusion is obvious that the most satisfactory method of designating minimum legal mesh sizes of pound nets and deep trap nets is on the basis of mesh size "as found in use." The wide experience of most commercial fishermen with different kinds of webbing and preservatives is certainly sufficient to preclude excessive losses as the result of undue shrinkage of their twine.

SUMMARY

1. The present investigation of the whitefish fishery of Lakes Huron and Michigan was undertaken because of the threat to the whitefish stocks offered by the introduction and rapid expansion in the use of a new and tremendously efficient gear, the deep trap net. This net, which was developed in Lake Ontario, was introduced into Lake Huron off Alpena, Mich., in 1928. Beginning in 1930, the use of the deep trap net expanded rapidly throughout the State of Michigan waters of Lake Huron and northern Lake Michigan. Operations with this gear were relatively limited in other waters (Wisconsin waters of Lake Michigan; Indiana waters of Lake Michigan; Michigan waters of Lake Superior and southern Lake Michigan). The greatest development of the deep-trap-net fishery occurred in the Michigan waters of central and southern Lake Huron.

2. The investigation was carried out along the following general lines:

a. A review of the available statistics on the production of whitefish in Lakes Huron and Michigan over the period, 1879-1939.

b. A detailed analysis of the fluctuations in the production and abundance of whitefish and in the intensity of the whitefish fishery in the different areas of the Michigan waters of Lakes Huron and Michigan in the years, 1929–1939, with special reference to the effects of the operations with deep trap nets. The methods of analysis are described.

c. A study of the bathymetric distribution of whitefish of legal and illegal size in order to obtain data on which to base recommendations for possible restrictions on the depth of water in which deep trap nets may be fished.

d. Observations in the field on the fishing action of pound nets and deep trap nets—particularly on the extent of the destruction of undersized whitefish. The field work was carried out in 1931 and 1932.

3. Although the fluctuations in the yield of whitefish in the various areas of Lakes Huron and Michigan over the period, 1879–1939, were by no means the same, certain general trends may be described. Production was high in all areas in the early years of the period. Later declines brought the catch to a much lower, and in some waters remarkably stable, level about which the production fluctuated for several decades. A pronounced general increase in the yield of whitefish occurred in the late 1920's and/or early 1930's. This increase was relatively greater and the subsequent decline was relatively more severe in the State of Michigan waters of Lake Huron than in other regions of the Great Lakes. Graphical representations of the history of whitefish production in different areas of Lakes Huron and Michigan are given in figures 2 and 3.

4. The increase in the abundance of whitefish that occurred in the late 1920's and early 1930's complicated greatly the problem of detecting the effects of deep-trap-net operations on the whitefish fishery of the State of Michigan waters of Lakes Huron and Michigan. This increase would have brought about a rise in both fishing intensity and catch even had deep trap nets not been introduced. Furthermore, a decline from this abnormally high level of yield and abundance was logically to be expected; the mere occurrence of a decline could not be interpreted as the result of the use of deep trap nets.

5. Despite this difficulty, the following observations demonstrated conclusively the disastrously harmful effects of extensive deep-trap-net operations on the stocks of whitefish:

a. The regions in which the deep-trap-net fishery underwent its greatest expansion (the four southernmost statistical districts of Lake Huron—see fig. 4) suffered an unreasonable multiplication of fishing intensity. In these districts of central and southern Lake Huron (H-3 to H-6) the maximum yield of whitefish was 4.3 to 26.6 times the 1929 catch; the maximum fishing intensity was 3.8 to 42.1 times the 1929 intensity. In the two northerly districts (H-1 and H-2)—areas in which the use of deep trap nets was much less extensive—the respective maximum productions were only 2.6 and 3.2 times the 1929 catch; the maximum fishing intensity was 2.3 times that of 1929 in each district.

b. In all districts of Lake Huron the introduction of the deep trap net brought about a tremendous increase in the catch of whitefish. After about two years of high production the catch fell sharply. This decrease in yield was accompanied by a rapid decline in the abundance of whitefish. However, these declines were relatively greater in central and southern Lake Huron. The 1939 production of whitefish, expressed as a percentage of the 1929 catch, was 38 in H-1 and 23 in H-2. These percentages were only 1 and 5 in H-3 and H-4. In H-5 and H-6 the 1939 yields were only 19 and 46 percent, respectively, of the 1929 production despite fishing intensities that were 4.3 and 4.9 times those of 1929. The 1939 abundance of whitefish, expressed as a percentage of the 1929 abundance, was 41 in H-1 and 43 in H-2. In central and southern Lake Huron these percentages were: H-3, 6; H-4, 7; H-5, 5; H-6, 10. These figures demonstrate that whereas the whitefish fishery merely declined in those districts (H-1 and H-2) in which the use of the deep trap net was relatively moderate, it collapsed in the districts (H-3 to H-6) in which deep-trap-net operations underwent their greatest expansion. The excessive use of deep trap nets, therefore, may be stated positively to be the cause of the present critical condition of the whitefish fishery in Lake Huron. The severity of the depletion is illustrated by the fact that the 1939 production of only

255,000 pounds was less than half the previously reported all-time low (555,000 pounds in 1900).

c. The statistics of the whitefish fishery of northern Lake Michigan (districts M-1, M-2, and M-3) for the years, 1929-1939, lend support to the conclusions based on the data for Lake Huron. In these Lake Michigan districts as in H-1 and H-2 the development of the deep-trap-net fishery may be termed relatively moderate. Although the whitefish fishery of northern Lake Michigan underwent a decline—a decline to which the use of deep trap nets may have contributed substantially—the severity of the decreases did not approach that of the decreases of central and southern Lake Huron; rather the changes resembled those that took place in northern Lake Huron. The deep trap net was of no significance in the State of Michigan waters south of district M-3, except in M-7 where it was the dominant gear for the production of whitefish in the single year, 1934.

6. The harmful effects of the deep-trap-net fishery can be traced to its great efficiency for the capture of whitefish in comparison with pound nets and large-mesh gill nets. Pound nets, which are held in position by stakes driven into the bottom of the lake, occupy the same position throughout the season, can be set only on soft bottom, and seldom are fished in water deeper than 60 feet. Deep trap nets, which are held in position by anchors and buoys, can be set on almost any kind of bottom and can be moved readily to any depth of water in which whitefish occur abundantly. These characteristics of the gear made possible the heavy exploitation of the whitefish at the time of their summer concentration in relatively deep water—far beyond the reach of pound nets. Gill nets have long been fished in these depths of the summer concentration of whitefish but in the modern fishery this gear has proved to be relatively unsuccessful for the capture of whitefish, except under certain special conditions (as during the spawning run or in limited local areas).

7. Records of the catch per lift of deep trap nets revealed that the gear was much less successful in northern Lake Huron (districts H-1 and H-2) and Lake Michigan (districts M-1, M-2, M-3, and M-7) than in central and southern Lake Huron (H-3 to H-6). This situation doubtless accounted in part (see p. 339) for the relatively less extensive development of the deep-trap-net fishery in Lake Michigan and northern Lake Huron.

8. Counts of legal- and illegal-sized whitefish in lifts of pound nets and deep trap nets from different depths of water were employed in a study of the bathymetric distribution and vertical movements of the species during the summer and early autumn.

9. The combined data for the months, May to October, inclusive, indicated that legal-sized whitefish were most abundant in Lake Huron at depths of 81 to 110 feet with the peak concentration in 91 to 100 feet. Illegal-sized fish were most abundant in 71 to 110 feet with a maximum concentration at 81 to 90 feet, 10 feet shallower than the depth of greatest abundance of legal fish. The records for the grounds off Alpena and in the Saginaw Bay area suggest that both legal- and illegal-sized whitefish may move onshore during the summer and return to deeper water in the autumn.

10. The whitefish lives in shallower water in northern Lake Michigan than in Lake Huron. The averages for the entire season (May to October, inclusive) showed legal-sized whitefish to be most abundant in 71 to 110 feet (peak concentration at 81-90 feet) and illegal-sized fish in 61 to 110 feet (peak at 71-80 feet). The depths of the peak concentrations were 10 feet shallower in northern Lake Michigan than in Lake Huron for fish of corresponding size.

11. The records for the individual months indicated that both legal- and illegal-sized whitefish in northeastern Lake Michigan moved toward deeper water from June to September. The October data provided some indication of a return migration in the autumn. These movements are the reverse of those indicated by the data for the Lake Huron whitefish.

12. The vertical distribution of whitefish in northeastern Lake Michigan was characterized by the presence of two concentration zones of both legal- and illegal-sized fish. Although the actual depths at which the zones occurred varied from month to month with the offshore and onshore movements of the fish, the two concentrations remained

distinct nevertheless in every month but September in the 5-month period, June to October. The inshore and offshore concentrations of legal-sized whitefish were separated by a difference in depth of 20 feet in each of the four months in which both were present. The offshore concentration of illegal-sized whitefish was 30 feet deeper than the inshore concentration in June, July, and August, but was only 20 feet deeper in October.

13. The persistent occurrence of two concentration zones of whitefish in northeastern Lake Michigan throughout most of the summer and early autumn raises the question of the possible existence of distinct inshore and offshore populations or races. Arguments were outlined briefly for and against this interpretation of the two concentrations; available data do not, however, permit a definite decision.

14. On the basis of the observations on the bathymetric distribution of whitefish, it was suggested that young fish would be protected from excessive handling and possible destruction and legal-sized fish from ruinous exploitation if the operations of deep trap nets were limited in Lake Huron to depths of 80 feet and less and in Lake Michigan to depths of 70 feet and less. The proposed restriction has been effective in Lake Huron since August 1, 1934; the use of deep trap nets was made illegal in Lake Michigan after 1935.

15. A limited amount of information was presented on the bathymetric distribution and seasonal movements of the lake trout, yellow pike, burbot, white sucker, and long-nosed or sturgeon sucker.

16. Comparisons of the average numbers of fish per lift of large-mesh (meshes of 4 inches or more, extension measure, in the pot) and small-mesh (less than 4 inches) pound nets and deep trap nets operated under comparable conditions (on the same grounds, in the same calendar year and month, and in the same depth of water) revealed that in general the large-mesh nets took the greater numbers of legal-sized whitefish and the lesser numbers of illegal-sized individuals. Large-mesh nets took 31.3 percent fewer undersized whitefish than did small-mesh nets that captured an equal number of legal-sized fish. Further evidence for the escape of undersized whitefish from the nets with larger mesh sizes was provided by the regular increase, with increase in the size of mesh, in the average length and weight of illegal-sized whitefish captured in pound nets and deep trap nets or gilled in the meshes of the lifting pot. On the basis of the selectivity data a minimum mesh size of $4\frac{1}{2}$ inches or greater (extension measure as found in use) in the pots was recommended for pound nets and deep trap nets employed for the capture of whitefish and lake trout. (This size of mesh is prescribed by the present State of Michigan law.) Although the data indicated that meshes of $4\frac{1}{2}$ inches or more will permit the escape of the smaller legal-sized lake trout, a smaller mesh cannot be recommended because lake trout and whitefish ordinarily are taken together. Furthermore, data on the size of lake trout at first maturity indicate the need for an increase in the size limit (now $1\frac{1}{2}$ pounds) rather than a decrease in the minimum legal mesh size of pound nets and deep trap nets.

17. Observations of the lifting of pound nets and deep trap nets did not indicate the destruction of illegal-sized whitefish to be excessive even in those areas in which it was estimated that hundreds of thousands of young fish were captured in a single season. The "known" destruction of undersized fish (individuals dead from gilling or other causes at the time of lifting) ranged from 2.40 to 3.80 percent according to the lake, type of net, and size of mesh. These percentages tended to be higher for deep trap nets than for pound nets. To the "known" destruction must be added the undetermined losses from the later death of live bloated fish (only a little more than 1 percent of the live illegal-sized whitefish were bloated) and of fish killed or injured fatally during the sorting of the catch. Field observations indicated, however, that most (but not all) fishermen attempted to avoid rough handling of small whitefish and returned them to the water as soon as possible.

18. Extensive measurements were obtained of meshes in the pots of pound nets and deep trap nets in order to determine the amount of shrinkage produced by different types of preservatives applied to the twine. No significant difference could be found between the shrinkage brought about by treatment with tar and copper oleate. The mesh size

of treated nets averaged a little less than a half inch smaller than the mesh size as manufactured. The amount of shrinkage varied widely, however, in the individual nets. Because of this variation the minimum legal size of mesh should be specified "as found in use" rather than "as manufactured." Once a net has been treated, it is impossible to determine exactly the original size of the mesh.

APPENDIX A

SOURCES OF THE DATA ON PRODUCTION, 1879-1939

The following paragraphs contain the details concerning the sources of the production data of table 1. Where more than one source was available for any single year, preference usually was given to that with the most continuous record over a period of years.

(1) Sessional Papers of the Parliament, Dominion of Canada: all data for the Canadian waters of Lake Huron, 1879-1905.

(2) Annual Reports of the Game and Fisheries Department of the Province of Ontario: all data for the Canadian waters of Lake Huron, 1906-1939.

(3) Reports of the United States Commissioner of Fisheries and his administrative successors: all data for United States waters, 1879 (repeatedly listed erroneously in the reports as for 1880) and 1885; United States waters, except the Wisconsin waters of Lake Michigan, 1890 (including the total for the Lake); Wisconsin waters of Lake Michigan, 1926-1939; total for Lake Michigan, 1925; Indiana and Illinois waters of Lake Michigan, 1879, 1885, 1890, 1897, 1903, 1917, 1922, and 1925-1939 (actually, no whitefish catch was reported from these States in 1938 and 1939). The Indiana and Illinois catches of whitefish in Lake Michigan for the above years, although not recorded in table 1, have been included in the Lake Michigan totals. All other Lake Michigan totals for individual years, except 1889 and 1908, are exclusive of the Indiana and Illinois catches.

(4) Reports of the State of Michigan Department of Conservation and its administrative predecessors: State of Michigan waters of Lake Michigan, 1911; State of Michigan waters of Lakes Huron and Michigan, 1912-1928.

(5) United States Bureau of the Census—Fisheries of the Great Lakes, Census Bulletin no. 173: all United States waters (including catches in Illinois and Indiana), 1889. Fisheries of the United States, Special Report: Wisconsin waters of Lake Michigan, 1908; Indiana and Illinois waters of Lake Michigan, 1908 (not listed in table 1 but included in the total for the lake).

(6) Compilations made from original State records:

Wisconsin.—Wisconsin waters of Lake Michigan, 1890, 1892-1897, 1899, 1903, and 1909-1925.

Michigan.—Michigan waters of Lakes Huron and Michigan, 1891-1908.

Michigan.—Compilations from the daily reports of commercial fishermen—State of Michigan waters of Lakes Huron and Michigan, 1929-1939. (These data are treated in detail in part II.)

Although certain data are available for earlier years, the statistical records for the whitefish fisheries of the United States waters of Lakes Huron and Michigan may be assumed for practical purposes to begin with 1889 and 1891. The 1879, 1885, and 1890 catches included longjaws, blackfins, and Menominee whitefish in Lake Michigan, and Menominee whitefish in Lake Huron. The only clue as to the extent of the errors brought about by these inclusions is provided by the fact that in 1890 longjaws, blackfins, and Menominee whitefish made up about 26 percent of the reported catch of whitefish in Lake Michigan (1,398,238 pounds in a total of 5,455,079 pounds). The 1890 total for the Wisconsin waters of Lake Michigan is based on State records and is not known to include any species other than whitefish. However, Wisconsin contributes a relatively small part of the total whitefish catch in Lake Michigan.

As has been mentioned previously, the Lake Michigan totals for several individual years do not include the catch of whitefish in Indiana and Illinois waters. However,

the error involved is small, as the following catches for the years in which the production in these two States is known will show:

Year	Pounds	Year	Pounds	Year	Pounds
1885.....	¹ 247,086	1922.....	20,800	1933.....	6,600
1889.....	37,375	1926.....	12,094	1934.....	4,600
1890.....	² 94,736	1927.....	22,436	1935.....	1,500
1897.....	³ 39,760	1928.....	15,454	1936.....	6,500
1899.....	10,558	1929.....	36,375	1937.....	3,800
1903.....	2,905	1930.....	10,695	1938.....	No catch
1908.....	65,000	1931.....	9,755	1939.....	do.
1917.....	37,750	1932.....	12,450		

¹ Includes longjaws, blackfins, and Menominee whitefish.

² Includes longjaws, blackfins, and Menominee whitefish—the total listed for the lake does not, however, include these species.

³ Fiscal year.

The tabulation of the statistics of the production of whitefish in the Canadian waters of Lake Huron has been started with 1879, the first year for which statistics are available for United States waters. Available statistics on the production of whitefish in the Canadian waters of Lake Huron for the earlier years, 1867–1878, have been omitted from table 1 because of the lack of comparative data for United States waters. These earlier Canadian records also are open to the criticism that in a number of years the production reported for Huron proper included the catch in the St. Clair River and in Lake St. Clair to the point of inflow of the Thames River. The catches listed under "Huron proper" for the years, 1879–1921, were taken between the tip of the Saugeen Peninsula at Cape Hurd, Ontario, and the extreme southern end of Lake Huron. Beginning in 1922 the islands of the open lake and the westerly shore of Manitoulin Island to the north of the Saugeen Peninsula were included in "Huron proper."

As stated in footnote 8, the catches listed under the heading, "Georgian Bay," represent a combination of the take in the Bay and in the North Channel and Manitoulin Island regions to the north and west except in 1922 and later years as explained above. This combination was made partly in an attempt to reduce the size and complexity of table 1 and partly because of variation in the extent of the waters included in the two areas. For example, reports for certain of the earlier years listed the catches along the east shore of Georgian Bay as far south as Penetanguishene as part of the production in the Manitoulin Island and North Channel area.

Reference should be made here to the Canadian records compiled for the International Board of Inquiry for the Great Lakes Fisheries and published after this manuscript was completed.⁴¹ The districts employed by Ford are not always the same as those used in this report and her statistics for these areas are therefore not always comparable with ours. However, both records of the total Canadian catch of Lake Huron should be the same. Minor discrepancies occur for some years because, in contrast to our records, Ford's figures were rounded to the nearest hundredweight. In other years the discrepancies are larger, though still insignificant. The reason for these differences is not known. A check with the published records of the Game and Fisheries Department of Ontario reveals that our figures agree with theirs. At any rate our conclusions would remain the same whether we utilized Ford's data or our own.

The accuracy of the catches recorded for the Ontario waters of Huron proper in 1908 and 1909 has been considered so questionable that the values were not plotted in figure 2 and were omitted in the computation of averages for periods that included these 2 years. The contrast between the catches for 1908 and 1909 and the production in the years immediately preceding and immediately following is in itself sufficiently great to give just grounds for suspicion. This suspicion is heightened by the observation that the large 1908 and 1909 catches are to be traced to reports of excessive quantities of whitefish as barrels of salt whitefish. In 1908 3,515 barrels (703,000 pounds) and in 1909 550 barrels (110,000 pounds) of salt whitefish were reported. In other years of the period, 1900–1917, the number of barrels of salt whitefish reported for Huron proper did not exceed 82, and averaged only 12 barrels.

Barrels of salt fish have been converted to fresh fish at the rate of 200 pounds per barrel. Catches given as numbers of fish have been converted to pounds at the rate of 2 pounds per fish.

⁴¹ International Board of Inquiry for the Great Lakes Fisheries. Report and Supplement. Washington, 1943.

Ford, Marjory A. Annual Landings of Fish on the Canadian Side of the Great Lakes from 1867 to 1939 as Officially Recorded. Ottawa, 1943

APPENDIX B DETAILED STATISTICS ON WHITEFISH PRODUCTION IN STATE OF MICHIGAN WATERS OF LAKES HURON AND MICHIGAN, 1929-1939

TABLE 48.—*Production of whitefish in pounds according to gear in the several districts of the State of Michigan waters of Lakes Huron and Michigan, 1929-1939*

[The districts of Lake Huron are numbered H-1, H-2, *** and of Lake Michigan, M-1, M-2, ***. In districts M-4, M-5, M-6, and M-8 the catch of deep trap nets is included under "Other."]

DISTRICT H-1						
Year	Gear				Total annual production	Percentage of average annual production
	Large-mesh gill net	Deep trap net	Pound net	Other		
1929	232,063		142,182	1,332	375,577	81
1930	174,851	386,453	291,765	2,293	755,362	163
1931	246,897	375,122	337,805	27,642	987,466	213
1932	135,059	170,313	306,938	11,360	623,670	135
1933	121,664	64,251	161,133	18,635	365,683	79
1934	105,582	104,699	166,877	947	378,105	82
1935	106,498	163,465	98,512	4,399	372,874	80
1936	82,464	346,821	100,282	11,825	541,392	117
1937	43,626	236,196	93,428	505	373,755	81
1938	54,834	73,184	51,035	1,074	180,127	39
1939	40,368	73,406	25,876	1,401	141,051	30
Average 1929-1939	122,173	172,174	161,439	7,401	463,187	100

DISTRICT H-2						
Year	Large-mesh gill net	Deep trap net	Pound net	Other	Total annual production	Percentage of average annual production
1929	12,708	87,121	173,904	907	274,640	160
1930	48,151	358,872	187,443	60	594,526	345
1931	18,252	376,887	83,679	151	478,969	278
1932	3,785	94,527	18,823	297	117,432	68
1933	5,641	28,540	22,386	178	56,745	33
1934	7,331	44,153	39,041	2,591	93,116	54
1935	3,653	94,584	19,025	1,025	118,287	69
1936	1,197	46,602	3,346	4,461	55,606	32
1937	1,923	14,009		4,881	20,813	12
1938	25	34,315	229	6,794	41,363	24
1939	8	41,980		297	42,285	25
Average 1929-1939	9,334	111,054	49,807	1,967	172,162	100

DISTRICT H-3						
Year	Large-mesh gill net	Deep trap net	Pound net	Other	Total annual production	Percentage of average annual production
1929	43,426		54,536	856	98,818	107
1930	63,216	157,248	21,998	5,110	247,572	269
1931	44,336	395,230	7,121	23,736	470,423	511
1932	7,644	85,236	475	44,108	137,463	149
1933	4,218	9,912			14,130	15
1934	1,791	12,558		50	14,399	16
1935	928	7,964	9	6	8,907	10
1936	439	7,567			8,006	9
1937	799	1,934		65	2,798	3
1938	187	8,910	42	24	9,163	10
1939	230	277		50	557	1
Average 1929-1939	15,201	62,440	7,653	6,728	92,022	100

DISTRICT H-4						
Year	Large-mesh gill net	Deep trap net	Pound net	Other	Total annual production	Percentage of average annual production
1929	85,186		437,848	48,571	571,605	83
1930	137,402	68,748	757,720	79,525	1,043,395	152
1931	96,986	932,357	446,010	472,732	1,948,085	283
1932	46,400	1,934,325	224,285	257,948	2,462,958	358
1933	2,969	620,125	105,255	33,213	761,562	111
1934	4,687	116,849	44,192	29,217	194,945	28
1935	183	138,446	51,002	22,882	212,513	31
1936		75,438	21,829	31,450	128,717	19
1937	260	121,796	12,716	20,319	155,091	23
1938	158	38,224	5,708	11,795	55,885	8
1939	176	18,785	2,319	4,665	25,945	4
Average 1929-1939	34,037	369,554	191,717	92,029	687,337	100

TABLE 48.—*Production of whitefish in pounds according to gear in the several districts of the State of Michigan waters of Lakes Huron and Michigan, 1929-1939—Continued*

[The districts of Lake Huron are numbered H-1, H-2, *** and of Lake Michigan, M-1, M-2, ***. In districts M-4, M-5, M-6, and M-8 the catch of deep trap nets is included under "Other."]

DISTRICT H-5

Year	Gear				Total annual production	Percentage of average annual production
	Large-mesh gill net	Deep trap net	Pound net	Other		
1929	61,052		1,935		62,987	19
1930	84,803		4,879	1,811	91,493	27
1931	66,647		6,125	1,266	74,038	22
1932	29,080	479,916	4,413		513,409	152
1933	15,114	1,658,753	2,565		1,676,432	496
1934	253	783,606	345	11	784,215	232
1935	270	272,746	405		273,421	81
1936		119,103	37		119,140	35
1937	137	66,688			66,825	20
1938	83	41,832			41,915	12
1939		12,247			12,247	4
Average 1929-1939	23,404	312,263	1,882	281	337,830	100

DISTRICT H-6

1929	55,526		13,291	3,924	72,741	19
1930	105,329		38,781	2,982	147,092	37
1931	146,397		30,200	4,194	180,791	46
1932	163,598		14,764	17,040	195,402	50
1933	119,665	322,995	13,890	2,799	459,349	117
1934	70,057	999,618	7,752	26,026	1,103,453	281
1935	21,257	810,137	3,327	74,084	908,805	232
1936	4,851	571,176	1,606	11,675	589,308	150
1937	3,192	393,541	1,077	1,589	399,399	102
1938	390	226,608	1,799	719	229,516	58
1939	290	31,822	716	270	33,098	8
Average 1929-1939	62,777	305,082	11,564	13,209	392,632	100

DISTRICT M-1

1929	596,743		535,227	7,658	1,139,628	217
1930	582,761	37,655	445,969	9,363	1,075,748	205
1931	500,828	111,523	575,457	7,161	1,194,969	227
1932	353,998	191,979	344,086	20,043	910,106	173
1933	72,722	77,161	85,755	2,531	238,169	45
1934	74,682	56,918	130,407	998	263,005	50
1935	97,241	22,783	50,246	4,367	174,637	33
1936	51,937		37,899	367	90,203	17
1937	54,767		50,039	83	104,889	29
1938	233,314		120,829	92	354,235	68
1939	100,381		136,660	468	237,509	45
Average 1929-1939	247,216	45,274	228,416	4,830	525,736	100

DISTRICT M-2

1929	62,339		27,678	2	90,019	164
1930	84,555		16,070		100,625	184
1931	55,593	13,645	12,374	6	81,618	149
1932	26,610	59,303	1,330	5	97,248	178
1933	11,288	30,753	236		42,277	77
1934	15,278	11,580			26,858	49
1935	42,643	3,621			46,264	85
1936	46,465				46,465	85
1937	31,489			4	31,493	57
1938	24,221				24,221	44
1939	15,402				15,402	28
Average 1929-1939	38,717	10,809	5,244	2	54,772	100

DISTRICT M-3

1929	805,344		1,396,439	281	2,202,064	206
1930	920,784	97,454	1,442,083	335	2,460,656	230
1931	484,121	273,282	622,686	361	1,380,450	129
1932	430,866	596,246	462,360		1,489,472	140
1933	277,322	318,260	295,309	8	890,899	83
1934	251,308	251,012	259,511		761,831	71
1935	368,955	177,374	202,793	544	749,666	70
1936	289,502		156,446	19	445,967	42
1937	297,274		153,176	169	450,619	42
1938	294,479		203,261	36	497,776	47
1939	228,482		196,998	15	425,495	40
Average 1929-1939	422,585	155,784	490,097	161	1,068,627	100

TABLE 48.—*Production of whitefish in pounds according to gear in the several districts of the State of Michigan waters of Lakes Huron and Michigan, 1929-1939—Continued*

[The districts of Lake Huron are numbered H-1, H-2, *** and of Lake Michigan, M-1, M-2, ***. In districts M-4, M-5, M-6, and M-8 the catch of deep trap nets is included under "Other."]

DISTRICT M-4

Year	Gear				Total annual production	Percentage of average annual production
	Large-mesh gill net	Deep trap net	Pound net	Other		
1929	30,433		42,158	38	72,629	127
1930	41,335		42,784		84,119	147
1931	43,753		40,235	265	84,253	148
1932	44,552		32,857	1,362	78,771	138
1933	22,683		26,758	1,569	51,010	89
1934	6,435		41,386	548	48,369	85
1935	7,663		35,864	4,451	47,978	84
1936	26,807		29,377	50	56,234	98
1937	16,671		27,179	16	43,866	77
1938	17,707		11,525	17	29,249	51
1939	18,735		13,022	10	31,767	56
Average 1929-1939	25,161		31,195	757	57,113	100

DISTRICT M-5

1929	271,324		13,296		284,620	89
1930	259,351		21,345	5	280,701	88
1931	548,048		32,488		580,536	183
1932	532,784		21,992	3,797	558,573	176
1933	493,070		33,070	3,557	528,697	167
1934	272,782		25,675	40	298,497	94
1935	198,864		9,790	153	208,607	66
1936	189,741		9,013	47	198,801	62
1937	263,057		4,236	92	267,385	84
1938	176,421		13,203	34	189,658	60
1939	90,359		6,899	10	97,268	31
Average 1929-1939	299,618		17,364	703	317,685	100

DISTRICT M-6

1929	102,934		463		103,397	141
1930	140,707		80,916	525	222,148	304
1931	195,233		47,905	8,877	252,015	345
1932	77,457		7,450	173	85,080	116
1933	37,498		3,058	2,625	43,181	59
1934	29,405		4,125	3,920	37,450	51
1935	24,415		444	2	24,861	34
1936	9,998		4,065		14,063	19
1937	10,887		210	3	11,100	15
1938	4,717		2,070		6,787	9
1939	2,600		2,037	16	4,653	7
Average 1929-1939	57,805		13,886	1,467	73,158	100

DISTRICT M-7

1929	123,905		15,647	138	139,690	135
1930	202,878		244,882		447,760	433
1931	41,836	347	65,023		107,206	104
1932	24,096	3,819	19,970	49	47,934	46
1933	118,728	6,240	32,725	6	157,699	153
1934	66,400	74,956	49,178	48	190,582	184
1935	26,090	3,079	638	699	30,506	30
1936	4,243		893	76	5,212	5
1937	7,306		705	6	8,017	8
1938	550		559	28	1,137	1
1939	1,022		471	44	1,537	1
Average 1929-1939	56,096	8,040	39,154	99	103,389	100

DISTRICT M-8

1929	251,071		1,175	3,576	255,822	197
1930	106,791		34,277		141,068	108
1931	117,167		25,408	361	142,936	110
1932	64,142		622	336	65,100	50
1933	274,632		8,276		282,908	217
1934	284,784		20,788	14	305,586	235
1935	145,208		1,592	2,205	149,005	114
1936	16,591		2,815	60	19,466	15
1937	28,064		982	452	29,498	23
1938	14,007			9	14,016	11
1939	25,820		401	4	26,225	20
Average 1929-1939	120,752		8,758	638	130,148	100

APPENDIX C

INVESTIGATION OF POUND NETS AND DEEP TRAP NETS IN THE
WISCONSIN WATERS OF LAKE MICHIGAN, 1931⁴²

The brief investigation of the pound-net and deep-trap-net fisheries of the Door peninsula was conducted for the specific purpose of determining the validity of the strenuous complaints of commercial fishermen against the use of the deep trap net. The objections against the deep trap net as a dangerously efficient gear, as a source of destruction to young fish, and as a usurper of pound-net grounds were in general the same as those put forward by Michigan fishermen, and, consequently, need not be outlined in detail here. (See p. 298.) The procedure of the investigation involved observations of the lifting of pound nets and deep trap nets, interviews with operators of both types of nets (including a public hearing attended by more than 250 fishermen at Fish Creek, July 10, 1931), and the compilation of statistics on (1) the production of whitefish in the Wisconsin waters of Green Bay and Lake Michigan, beginning in 1889, and (2) the production of whitefish and the catch per lift in pound nets and deep trap nets of the Door peninsula, 1930-1931.

PRODUCTION OF WHITEFISH IN THE GREEN BAY AND LAKE
MICHIGAN WATERS OF WISCONSIN, 1889-1939

The data on whitefish production in the State of Wisconsin waters of Green Bay and Lake Michigan (table 49) were compiled from original records in the files of the Wisconsin Conservation Department.⁴³

TABLE 49.—*Production of whitefish in pounds in Green Bay and Lake Michigan, 1889-1939*

(Compiled from State records at Madison, Wis.)

Year	Green Bay	Lake Michigan	Green Bay and Lake Michigan	Year	Green Bay	Lake Michigan	Green Bay and Lake Michigan
1889.....	248,810	78,450	327,260	1920.....	42,411	89,022	131,433
1890.....	181,692	5,750	187,442	1921.....	171,896	190,519	362,415
1892.....	54,540	279,540	334,080	1922.....	80,658	82,543	163,201
1893.....	450,000	20,325	470,325	1923.....	74,484	363,439	437,923
1894.....	392,100	25,000	417,100	1924.....	182,989	64,115	247,104
1895.....	500,000	20,325	520,325	1925.....	147,556	94,823	242,379
1896.....	525,000	28,000	553,000	1926.....	249,976	90,479	340,455
1897.....	568,367	317,991	886,358	1927.....	191,779	122,453	314,232
1899.....	37,685	37,670	125,355	1928.....	430,386	123,681	554,067
1903.....	5,949	110,815	116,764	1929.....	287,648	44,965	332,613
1909.....	83,114	50,139	133,253	1930.....	500,996	34,832	535,828
1910.....	49,340	28,221	77,561	1931.....	462,117	235,663	697,780
1911.....	36,424	88,095	124,519	1932.....	183,002	93,522	276,524
1912.....	102,080	78,203	180,283	1933.....	86,051	37,402	123,453
1913.....	41,750	76,175	117,925	1934.....	82,105	-17,591	99,696
1914.....	21,435	19,230	40,665	1935.....			263,900
1915.....	60,835	60,081	120,916	1936.....	49,046	93,555	142,601
1916.....	12,049	96,172	108,221	1937.....	45,587	91,270	136,857
1917.....	20,853	106,080	126,933	1938.....	60,962	80,663	141,625
1918.....	21,012	233,067	254,079	1939.....	27,200	86,620	113,820
1919.....	83,184	118,935	202,119				

Green Bay.—Whitefish production was large in the early and middle nineties, but there was a sharp drop in the catch at about the turn of the century. Production remained rather consistently at a low level over the years, 1909-1923; only two years (1912 and 1921) of this period had yields in excess of 100,000 pounds. Beginning in 1924 the production of whitefish in Green Bay followed an irregular but definite upward trend that culminated in a yield of a half million pounds in 1930. This catch (1930) was the greatest since 1897 and was the third largest in the known history of the fishery.

⁴² This section is condensed from the unpublished "Report to the Conservation Commission of the State of Wisconsin on the Investigation of Deep Trap Nets, Conducted Jointly by the State Fisheries Department and the United States Bureau of Fisheries during the Period, July 6 to 11, 1931, in the Waters of Door County, Wisconsin." The investigation was made by Dr. John Van Oosten of the United States Bureau of Fisheries (now the Fish and Wildlife Service) and Messrs. B. O. Webster and Ira G. Smith of the Wisconsin Conservation Department.

⁴³ There are certain discrepancies between the data of table 49 of this appendix and those of table 1 of part I. These arise from the fact that the former table has been based entirely on State of Wisconsin records (in order to have data for Green Bay and Lake Michigan separately) whereas the records of whitefish production in Wisconsin waters in the latter table were obtained from several sources. (See appendix A.)

Production was still high in 1931; however, the years, 1932-1939, comprised a period of rapid decline. The 1939 catch of 27,200 pounds was the lowest since 1918.

Lake Michigan.—The Lake Michigan data are much more variable than those for Green Bay, and it is correspondingly difficult to speak of definite periods of high or low production. Frequently exceptionally good or poor years are isolated (as, for example, 1892 and 1931). The period of most consistently low production was 1909-1916 (all years below 100,000 pounds) and the most extended era of heavy yield was 1917-1923 (all but two years above 100,000 pounds). The best of the more recent years was 1931 with a catch of 236,000 pounds. The 1931 catch was exceeded by that of only one year (1923) since 1897 and was the fourth highest in the history of the fishery. Production was consistently below 100,000 pounds in the years, 1932-1939 (no data for 1935).

Green Bay and Lake Michigan.—The data for all of the State of Wisconsin waters of Lake Michigan show a fairly consistent high level of yield for the years, 1889-1897. Available data indicate a relatively low production in the period, 1899-1917; only once (1912) did the catch exceed 150,000 pounds in the 11 years for which there are records, and it fell below 100,000 pounds in 2 of them (1910 and 1914). An upturn occurred in 1918. Over the period, 1918-1925, production fell below 200,000 pounds only twice (1920 and 1922) and exceeded 400,000 pounds in 1923. A still higher level was maintained during the six years, 1926-1931. All of the annual yields were above 300,000 pounds and 3 years had catches in excess of 500,000 pounds. The 1931 take of 698,000 pounds was the largest since 1897 and the second largest in history. Production was at a relatively low level in the years, 1932-1939. The catch exceeded 200,000 pounds in only two of these years (1932 and 1935). The 1934 catch was the lowest since 1914 and the third lowest on record.

A striking feature of the State of Wisconsin data is the lack of agreement between the statistics for Green Bay and Lake Michigan. Some years were good or poor in both areas, as for example, 1897, 1931, and 1934. It is true also that the data for the two areas occasionally agreed rather well in general trend over a period of several years as in 1909-1917 and 1931-1934. On the other hand, there were numerous years that had a very high catch in one area and exceptionally poor production in the other. Outstanding examples of such disagreements occurred over the period, 1890-1896, and in the years 1918, 1923, 1926, 1929, and 1930.

POUND-NET AND DEEP-TRAP-NET FISHERY, 1930-1931

Table 50 contains data on the pound-net and deep-trap-net fisheries for whitefish in Door County waters, 1930-1931. (Practically all of Wisconsin's whitefish are produced in these waters.) The comparison of the average catch per lift of the two gears in corresponding months confirms the contention of fishermen that the deep trap net is the more effective gear. The catch per lift of deep trap nets was 2.7 times that of pound nets in May 1931, 2.2 times in June, and 2.3 times for May and June com-

TABLE 50.—*Production of whitefish and catch per lift in pound nets and deep trap nets of Door County, Wis., 1930-1931*

Date or period	Pound net			Deep trap net		
	Number of lifts	Production (pounds)	Catch per lift (pounds)	Number of lifts	Production (pounds)	Catch per lift (pounds)
<i>1930</i>						
May.....	285	23,427	88.4			
June.....	595	85,546	143.7			
May and June.....	860	108,973	126.7			
<i>1931</i>						
April.....				17	803	47.2
May.....	253	21,524	85.1	130	29,652	228.1
June.....	391	66,364	169.7	184	69,359	376.4
July.....				43	11,509	267.6
April to July.....				374	111,323	297.3
May and June.....	644	87,888	136.4	314	99,011	315.3

bined. The data do not, however, support the complaint that the deep-trap-net fishery was extremely harmful to the pound-net fishery in 1931. It is true that the total production in pound nets was less in 1931 than in 1930, but the decline was the result of reduced fishing intensity. The average catch of whitefish per lift of pound nets was approximately 10 pounds greater in 1931 than in 1930.

Although the average lifts of whitefish in deep trap nets in 1931 were 2.3 times those of pound nets, this advantage depended only on the greater depth of water in which deep trap nets were fished. The effect of the depth of water on the size of the lift is brought out by the comparison of the lifts of whitefish in shallow pound nets, deep pound nets (more than 50 feet of water), and deep trap nets (table 51). There was little difference between the size of the lifts of deep pound nets and deep trap nets, but both took more than 8 times as many fish per lift as shallow pound nets (less than 50 feet of water). It is obvious, therefore, that any indictment of the deep trap net in Door County waters as a dangerously effective gear must apply also to deep pound nets.⁴⁴

TABLE 51.—Comparison of the catch of whitefish of shallow pound nets, of deep pound nets, and of deep trap nets fished in Door County, Wisconsin waters, June 1931

Gear	Number of lifts	Total production (pounds)	Catch per lift (pounds)
Shallow pound net.....	58	2,566	44.2
Deep pound net.....	60	21,861	364.3
Deep trap net.....	184	69,359	376.4

Further conclusions based on observations of pound nets and deep trap nets in Door County waters are summarized as follows:

(1) The sorting of fish was more difficult in deep trap nets than in pound nets. However, less sorting was necessary with deep trap nets than with pound nets which ordinarily had 2-inch mesh (stretched measure). Very few illegal whitefish (legal size limit, 13 inches, total length, at the time of the investigation) were seen in deep trap nets, the mesh of which ranged from 3½ to 4½ inches. On several occasions small fish were seen to escape through the meshes as deep trap nets were lifted.

(2) Very few gilled fish were observed in deep trap nets, and most of the fish gilled were of legal size. A 3½-inch-mesh net allows the escape of whitefish of 13 to 13½ inches, total length, and smaller; 4½-inch meshes release whitefish about 16 inches long, and smaller.

(3) The observations did not support the contention that illegal whitefish brought to the surface in deep trap nets die. Small whitefish and herring were seen to pass through the bottom of the trap nets when they reached the surface, apparently uninjured and certainly not bloated.

REGULATIONS RECOMMENDED FOR THE DEEP TRAP NET IN WISCONSIN WATERS

The investigating committee submitted the following recommendations for the regulation of the deep trap net in Wisconsin waters (almost entirely direct quotation from report):

1. The size of the mesh in the lifting pot must be not less than 4½ inches but the side of the pot where fish are bagged may be of smaller mesh.
2. The length of the lead shall be not more than 50 rods.
3. A buoy must be attached to every anchor and each buoy must have a flag attached to it, extending not less than 30 inches above the surface of the water.
4. The shortest distance between strings of trap nets or between trap nets and pound nets shall be not less than one-half mile. A trap net as here defined refers to any part of the net constructed of webbing and includes the pot, tunnel, heart, and lead (not the anchors, ropes, buoys, and flags).

⁴⁴ Both gears can operate on the concentrations of whitefish at depths of 50 or 60 feet. Attempts of deep-trap-net fishermen to locate whitefish in deeper water (ca. 100 feet) were unsuccessful.

5. A trap net shall not be set in water more than 60 feet deep. A trap net under this ruling is the same as that defined under regulation no. 4.

6. No more than two trap nets shall be placed in one string and an open space free from netting of not less than 50 feet shall be left between the nets.

7. In the event of a dispute between a trap-netter and a pound-netter concerning the distance between nets, priority consideration shall be given the pound-netter if it is established that he has fished for several years the grounds where his nets had been set. Such consideration shall be given even though the trap-netter was the first to set his nets on the disputed grounds at the beginning of the season.

8. A trap net or a string of trap nets must be set approximately at a right angle to the shore line or shoal or reef.

9. Regulations 2, 4, 5, 6, and 8 have been recommended for trap nets on the assumption that they will be observed by pound-netters also. Enforcement is to be contingent on the adherence of pound-netters to these regulations.

APPENDIX D

THE WHITEFISH FISHERY OF LAKES HURON AND MICHIGAN, 1940-1942

Because of unavoidable delays in publication, statistics of the whitefish fishery have become available for three additional years (1940, 1941, and 1942) since the preparation of the main body of this paper and appendices A, B, and C. The data for these years are presented in this appendix. Discussion is brief and is concerned chiefly with the demonstration that the new information substantiates the conclusions drawn previously. Emphasis is placed on the detailed statistics for the State of Michigan waters although production data are given for other areas.

TABLE 52.—*Production of whitefish in pounds in the State of Michigan waters of Lake Huron, 1940-1942*

District or area	Year	Production in gear				Total	Percentage of total catch of lake	Percentage of 1929-1939 average
		Large-mesh gill net	Deep trap net	Pound net	Other			
H-1	1940	43,661	52,996	25,637	415	122,709	65.2	26
	1941	24,282	41,987	28,298	367	94,934	83.5	21
	1942	22,657	29,450	23,527	104	75,738	79.7	16
H-2	1940	149	11,421	11	790	12,371	6.6	7
	1941		3,384		466	3,850	3.4	2
	1942	818	343		5,914	7,075	7.4	4
Northern Lake Huron (H-1 and H-2)	1940	43,810	64,417	25,648	1,205	135,080	71.8	21
	1941	24,282	45,371	28,298	833	98,784	86.9	16
	1942	23,475	29,793	23,527	6,018	82,813	87.1	13
H-3	1940	28	1,282	4	435	1,749	0.9	2
	1941	10		10	459	479	0.4	1
	1942	668		48		716	0.7	1
H-4	1940	80	25,454	3,847	2,172	31,553	16.8	5
	1941	217	8,604	977	1,719	11,517	10.1	2
	1942	907	5,068	60	1,263	7,298	7.7	1
Central Lake Huron (H-3 and H-4)	1940	108	26,736	3,851	2,607	33,302	17.7	4
	1941	227	8,604	987	2,178	11,996	10.5	2
	1942	1,575	5,068	108	1,263	8,014	8.4	1
H-5	1940		8,702			8,702	4.6	3
	1941		633			633	0.6	10
	1942						0.0	0
H-6	1940		10,795	82	153	11,030	5.9	3
	1941	256	1,996	37	25	2,314	2.0	1
	1942	135	3,238	188	706	4,267	4.5	1
Southern Lake Huron (H-5 and H-6)	1940		19,497	82	153	19,732	10.5	3
	1941		2,629	37	25	2,947	2.6	10
	1942		3,238	188	706	4,267	4.5	1
Lake Huron (all 6 districts)	1940	43,918	110,650	29,581	3,965	188,114		9
	1941	24,765	56,604	29,322	3,036	113,727		5
	1942	25,185	38,099	23,823	7,987	95,094		4

¹ Less than 0.5.

WHITEFISH FISHERY OF LAKE HURON, 1940-1942

The downward trend in the production of whitefish in the State of Michigan waters of Lake Huron which got under way in 1933, and in 1939 had carried the annual yield to less than half the previously recorded minimum (555,000 pounds in 1900), continued through 1940-1942 (table 52 of this appendix—for further data on production see also table 1 of part I, tables 3, 4, 5, and 6 of part II, and appendix B). The production of 95,000 pounds in 1942 amounted to only 4 percent of the 1929-1939 average for Lake Huron,⁴⁵ and was only 2 percent of the 1931 maximum yield. Aside from unimportant increases in H-2, H-3, and H-6 in 1942 the trend was downward in all districts during the 3-year period.

With the exception of H-1, where the production percentages ranged from 16 to 26, the 1940-1942 yields of all districts amounted to only 7 percent (H-2 in 1940) or less of the 1929-1939 mean. The 1942 production was nil in H-5, a district that yielded 1,676,000 pounds of whitefish in 1933.

H-1 accounted for 65.2 to 83.5 percent of the total whitefish yield of the lake in 1940-1942. The only other district that yielded as much as 10 percent of the total in a single year was H-4 (1940 and 1941). The dominance of H-1 in this limited fishery was even more pronounced than in the early years, 1891-1908.

The progressive decline in production in the years, 1940-1942, can be attributed to a continued general decrease in fishing intensity (tables 53 and 54—see tables 8 and

TABLE 53.—*Annual fluctuations in the intensity of the fishery for whitefish in each district of Lake Huron, 1940-1942*

[Expressed as percentages of the average 1929-1939 intensity in the district]

District	Intensity as percentage of mean for district			District	Intensity as percentage of mean for district		
	1940	1941	1942		1940	1941	1942
H-1.....	54	48	23	H-4.....	35	13	9
H-2.....	28	7	4	H-5.....	18	1	(²)
H-3.....	(¹)	(¹)	3	H-6.....	14	3	2

¹ Inadequate data.

² No production.

TABLE 54.—*Annual fluctuations in the intensity of the whitefish fishery for all six districts of Lake Huron combined (third row from bottom of right half of table) and distribution of each year's intensity among the districts*

[The average annual intensity for the entire lake, 1929-1939, is 100.0. In parentheses are the intensity values of the deep-trap-net fishery. The value of one unit is 1/1,100 of the total expected catch of all districts, 1929-1939]

District or area	Intensity as percentage of mean for entire lake			District or area	Intensity as percentage of mean for entire lake		
	1940	1941	1942		1940	1941	1942
H-1.....	{ 11.3 (5.1)	{ 8.1 (3.2)	{ 4.8 (1.5)	H-5.....	{ 3.6 (3.6)	{ 0.1 (0.1)	{ (²)
H-2.....	{ 1.7 (1.7)	{ 0.5 (0.5)	{ 0.2 (0.2)	H-6.....	{ 3.9 (3.3)	{ 0.8 (0.7)	{ 0.6 (0.5)
Northern Lake Huron (H-1 and H-2).....	{ 13.0 (6.8)	{ 8.6 (3.7)	{ 5.0 (1.7)	Southern Lake Huron (H-5 and H-6).....	{ 7.5 (7.4)	{ 0.9 (0.8)	{ 0.6 (0.5)
H-3.....	{ (¹)	{ (¹)	{ 0.1 (0.0)	Lake Huron (all 6 districts).....	{ 28.7 (21.4)	{ 12.6 (7.1)	{ 7.7 (4.0)
H-4.....	{ 8.2 (7.2)	{ 3.1 (2.6)	{ 2.0 (1.8)				
Central Lake Huron (H-3 and H-4).....	{ 8.2 (7.2)	{ 3.1 (2.6)	{ 2.1 (1.8)	Percentage of intensity represented by deep trap nets.....	74.6	56.3	51.9

¹ Inadequate data.

² No production.

⁴⁵ In this appendix as in part II references to "Lake Huron," "Lake Michigan," "the entire lake," or "the lake" should be understood to mean the State of Michigan waters only, unless otherwise specified

TABLE 55.—*Annual fluctuations in the abundance of whitefish in the various districts and areas of Lake Huron, 1940-1942*

[Expressed as percentages of average 1929-1939 abundance. In the computation of percentages for areas of more than one district and for the entire lake, the abundance percentage for each district was weighted according to the percentage of the total 1929 production contributed by that district]

District or area	Abundance percentage in year			District or area	Abundance percentage in year		
	1940	1941	1942		1940	1941	1942
H-1.....	52	56	75	H-5.....	12	21	(²)
H-2.....	32	36	24	H-6.....	14	13	28
Northern Lake Huron (H-1 and H-2).....	44	48	53	Southern Lake Huron (H-5 and H-6).....	13	17	28
H-3.....	(¹)	(¹)	41	Lake Huron (all 6 districts).....	29	31	35
H-4.....	17	15	15				
Central Lake Huron (H-3 and H-4)	17	15	19				

¹ Inadequate data.

² No production.

9 of part II) brought about by a level of abundance (tables 55 and 56—see tables 10 and 11 of part II) that made profitable operations impossible.

Although the abundance percentages (table 55) and records of catch per unit effort (table 56) can not be considered very reliable for the districts in which the production reached extremely low figures, the data of table 55 nevertheless give some indication that with respect to the entire lake the abundance, which began to decline in 1932, reached its lowest level in 1940 (29 percent of the 1929-1939 average) and improved slightly in 1941 (31 percent) and 1942 (35 percent).⁴⁶ These small increases in the abundance percentages can not be taken as the basis for optimism concerning a possible early recovery of the whitefish fishery. On the contrary, it is to be considered most probable that the abundance and production of whitefish will continue to be low for years to come. The fishing intensity which was relatively low in all districts in 1940-1942 (table 53) and which had declined to 7.7 percent of average in 1942 for all districts combined (table 54) can not be expected to increase materially until abundance has risen to a level that permits profitable fishing. If a significant recovery occurs at all in the whitefish fishery of Lake Huron it may be expected to be slow. It is conceivable, of course,

TABLE 56.—*Annual fluctuation in the catch of whitefish per unit of fishing effort of gill nets, deep trap nets, and pound nets in the various districts of Lake Huron, 1940-1942*

Gear and unit of effort	District	Catch of whitefish (pounds) per unit of effort		
		1940	1941	1942
Gill net (unit lift of 10,000 feet).....	H-1.....	39.7	39.5	50.3
	H-2.....	10.1		37.9
	H-3.....			10.0
	H-4.....	2.9	3.2	11.8
	H-5.....			
	H-6.....		13.2	7.0
Deep trap net (unit lift of one net).....	H-1.....	45.1	57.8	84.9
	H-2.....	24.9	28.0	6.2
	H-3.....			
	H-4.....	29.5	27.8	23.8
	H-5.....	32.0	57.5	
	H-6.....	44.8	42.5	98.1
Pound net (unit lift of one net).....	H-1.....	32.2	30.0	40.9
	H-2.....	1.6		
	H-3.....			
	H-4.....	4.5	3.1	1.4
	H-5.....			
	H-6.....	1.2	1.8	11.1

⁴⁶ Tables 53, 54, 55, and 56 contain no figures for H-3 in 1940 and 1941 and for H-5 in 1942. In H-3 the small catches of whitefish in 1940 and 1941 were mostly reported by fishermen using a gear (shallow trap net) not considered in our estimations of abundance or by operators whose reports did not contain information on the amount of gear lifted. No whitefish were produced in H-5 in 1942.

that unusual conditions in the lake which permitted an abnormally high survival of young in one or more years may restore the stock at a much higher rate than the present depleted condition of the population would give reason to expect.

Not only did the Michigan production of Lake Huron continue its decline after 1939, but the Canadian yield showed a similar trend (table 57), although not to the same disastrous degree. In Lake Huron proper (see p. 304 for its boundaries) the Canadian catch fell to 92,000 pounds in 1940 and increased only 1,000 pounds in 1941. These records are the lowest two for these waters since 1922 and comprise 42 percent of the average catch (219,513 pounds) for the period, 1923–1939. In Georgian Bay (includes the North Channel—see p. 304) the take decreased progressively from 1,275,000 pounds in 1939 to 833,000 pounds in 1941, the lowest production recorded for this area at least since 1922. This figure represents 58 percent of the average yield (1,427,564 pounds) for the years, 1923–1939. In the Michigan waters the 1941 catch equaled only 6 percent of the average production (2,052,331 pounds) during the period, 1922–1937, a value considerably less than the comparable Canadian percentages of 42 and 58. The 1939–1941 records of total catch for all waters (United States and Canadian) represent the lowest three ever recorded for the lake.

TABLE 57.—*Production of whitefish in pounds in Lakes Michigan and Huron, 1939–1942*

Year	Lake Michigan			Lake Huron			
	Wisconsin	Michigan	Entire lake	Michigan	Ontario		Entire lake
					Huron proper	Georgian Bay	
1939.....	110,700	839,856	950,556	255,183	115,061	1,275,255	1,645,499
1940.....	196,600	754,115	954,815	188,114	92,403	1,006,082	1,286,599
1941.....	400,538	896,474	1,286,354	113,727	93,058	833,111	1,039,896
1942.....	279,363	1,061,056	1,340,419	95,094	-----	-----	-----

WHITEFISH FISHERY OF LAKE MICHIGAN, 1940–1942

The production of whitefish in the State of Michigan waters of Lake Michigan, which had declined irregularly from the modern peak of 4,813,000 pounds in 1930, reached an all-time recorded low of 754,000 pounds in 1940 (table 58—for further data on production see also table 1 of part I, tables 13, 14, 15, and 16 of part II, and appendix B). Although this yield amounted to only 32 percent of the 1929–1939 average, it was relatively much higher than the 1940 catch in Lake Huron (9 percent of the 1929–1939 mean—table 52). The take of whitefish in Lake Michigan improved substantially in 1941 (896,000 pounds; 38 percent) and 1942 (1,061,000 pounds; 46 percent). The 1940–1942 trend of production was consistently upward in northern and northeastern Lake Michigan (M–2, M–3, and M–4) and in the Grand Haven-Muskegon district (M–7), but was consistently downward in Green Bay (M–1) or irregular in the remaining districts (M–5, M–6, and M–8).

In all three years M–3 contributed considerably more than half of the total production (63.8, 58.4, and 67.5 percent in 1940, 1941, and 1942, respectively). The Green Bay district (M–1) ranked second each year but contributed a constantly decreasing percentage of the total (16.3, 12.9, and 8.7 percent). Third position was held by M–5 in 1940 and 1941 (11.5 and 10.0 percent) and by M–4 in 1942 (6.7 percent). The percentage of the total yield produced in the districts that ranked lower than third ranged from 7.5 percent in M–4 in 1941 to 0.1 percent in M–7 in 1940. It may be noted that the percentages of total production in the various districts in 1940–1942 resembled the corresponding figures for 1891–1908 much more closely than they did those for 1929–1939.

The abundance percentages, records of catch per unit of effort, and figures on fishing intensity (tables 59, 60, 61, and 62—see tables 17, 19, 20, and 21 of the main body of this paper) show that but for a low level of fishing intensity, production would have been much higher in 1940–1942, particularly in the last two years of the period. The abundance of whitefish which had dropped to an extremely low level in 1940 (23

TABLE 58.—*Production of whitefish in pounds in the State of Michigan waters of Lake Michigan, 1940-1942*

District or area	Year	Production in gear			Total	Percentage of total catch of lake	Percentage of 1929-1939 average
		Large-mesh gill net	Pound net	Other			
M-1-----	1940-----	50,170	71,015	1,618	122,803	16.3	23
	1941-----	73,707	41,982	63	115,752	12.9	22
	1942-----	66,654	25,884	8	92,546	8.7	18
M-2-----	1940-----	8,310	1,463	-----	9,773	1.3	18
	1941-----	25,883	-----	-----	25,883	2.9	47
	1942-----	60,494	-----	-----	60,494	5.7	110
M-3-----	1940-----	225,939	254,771	66	480,776	63.8	45
	1941-----	280,571	241,884	629	523,084	58.4	49
	1942-----	384,704	331,228	54	715,986	67.5	67
M-4-----	1940-----	28,726	11,572	37	40,335	5.3	71
	1941-----	28,435	39,024	28	67,487	7.5	118
	1942-----	26,277	44,108	261	70,646	6.7	124
Northern Lake Michigan (M-1, M-2, M-3, and M-4)-----	1940-----	313,145	338,821	1,721	653,687	86.7	38
	1941-----	408,596	322,890	720	732,206	81.7	43
	1942-----	538,129	401,220	323	939,672	88.6	55
Central Lake Michigan (M-5)-----	1940-----	85,118	1,970	6	87,094	11.5	27
	1941-----	89,132	280	10	89,422	10.0	28
	1942-----	57,802	-----	-----	57,802	5.4	18
M-6-----	1940-----	925	108	130	1,163	0.2	2
	1941-----	6,348	-----	-----	6,348	0.7	9
	1942-----	1,823	-----	62	1,885	0.2	3
M-7-----	1940-----	706	131	14	851	0.1	1
	1941-----	24,965	2,672	26	27,663	3.1	27
	1942-----	22,315	6,804	-----	29,119	2.7	28
M-8-----	1940-----	11,312	-----	8	11,320	1.5	9
	1941-----	36,460	4,375	-----	40,835	4.5	31
	1942-----	31,559	1,014	5	32,578	3.1	25
Southern Lake Michigan (M-6, M-7, and M-8)-----	1940-----	12,943	239	152	13,334	1.8	4
	1941-----	67,773	7,047	26	74,846	8.3	24
	1942-----	55,697	7,818	67	63,582	6.0	21
Lake Michigan (all 8 districts)-----	1940-----	411,206	341,030	1,879	754,115	-----	32
	1941-----	565,501	330,217	756	896,474	-----	38
	1942-----	651,628	409,038	390	1,061,056	-----	46

to 73 percent of the 1929-1939 average in the individual districts and 63 percent for the 8 districts combined—table 61) improved in every district in 1941. This general improvement was reflected in a rise in the abundance percentage from 63 to 91 for the lake as a whole. Further increases in 1942 in M-2, M-3, and M-8 more than compensated for declines in the remaining districts and carried the abundance percentage for all districts combined to the still higher level of 95. The abundance of whitefish was above the 1929-1939 average in three districts (M-4, M-6, and M-7) in 1941 and in five districts (M-2, M-3, M-4, M-7, and M-8) in 1942. Conspicuous among the percentages are the high value of 257 in M-6 in 1941 and the low figures of 45 and 34 in M-5 in 1941 and 1942. M-5 was the only district with abundance below 85 in 1941 or below 76 in 1942.

TABLE 59.—*Annual fluctuations in the intensity of the fishery for whitefish in each district of Lake Michigan, 1940-1942*

[Expressed as percentages of the average 1929-1939 intensity in the district]

District	Intensity as percentage of mean for district			District	Intensity as percentage of mean for district		
	1940	1941	1942		1940	1941	1942
M-1-----	38	30	27	M-5-----	71	64	55
M-2-----	47	48	91	M-6-----	4	5	4
M-3-----	67	61	64	M-7-----	5	23	27
M-4-----	108	96	126	M-8-----	18	44	27

TABLE 60.—*Annual fluctuations in the intensity of the whitefish fishery for all eight districts of Lake Michigan combined (bottom of right half of table) and distribution of each year's intensity among the districts*

[The average annual intensity for the entire lake, 1929-1939, is 100.0. The value of one unit is 1/1,100 of the total expected catch of all districts, 1929-1939]

District or area	Intensity as percentage of mean for entire lake			District or area	Intensity as percentage of mean for entire lake		
	1940	1941	1942		1940	1941	1942
M-1.....	8.3	6.5	5.8	M-6.....	0.1	0.1	0.1
M-2.....	1.2	1.3	2.4	M-7.....	0.2	0.8	1.0
M-3.....	31.4	28.8	29.9	M-8.....	1.0	2.3	1.4
M-4.....	2.9	2.5	3.3				
Northern Lake Michigan (M-1, M-2, M-3, and M-4).....	43.8	39.1	41.4	Southern Lake Michigan (M-6, M-7, and M-8).....	1.3	3.2	2.5
Central Lake Michigan (M-5).....	10.5	9.5	8.1	Lake Michigan (all 8 districts).....	55.6	51.8	52.0

TABLE 61.—*Annual fluctuations in the abundance of whitefish in the various districts and areas of Lake Michigan, 1940-1942*

[Expressed as percentages of average 1929-1939 abundance. In the computation of percentages for areas of more than one district and for the entire lake, the abundance percentage for each district was weighted according to the percentage of the total 1929-1939 production contributed by that district]

District or area	Abundance percentage in year			District or area	Abundance percentage in year		
	1940	1941	1942		1940	1941	1942
M-1.....	70	85	76	M-6.....	45	257	80
M-2.....	38	99	121	M-7.....	23	161	147
M-3.....	73	87	115	M-8.....	57	85	108
M-4.....	68	128	101				
Northern Lake Michigan (M-1, M-2, M-3, and M-4).....	71	88	103	Southern Lake Michigan (M-6, M-7, and M-8).....	43	152	114
Central Lake Michigan (M-5).....	40	45	34	Lake Michigan (all 8 districts).....	63	91	95

TABLE 62.—*Annual fluctuation in the catch of whitefish per unit of fishing effort of gill nets and pound nets in the various districts of Lake Michigan, 1940-1942*

Gear and unit of effort	District	Catch of whitefish (pounds) per unit of effort		
		1940	1941	1942
Gill net (unit lift of 10,000 feet).....	M-1.....	83.0	124.6	92.0
	M-2.....	16.7	35.2	43.1
	M-3.....	45.0	59.9	80.8
	M-4.....	27.4	33.6	30.6
	M-5.....	31.2	35.5	27.0
	M-6.....	19.5	98.1	30.7
	M-7.....	31.4	221.7	161.1
	M-8.....	59.4	91.5	113.5
Pound net (unit lift of one net).....	M-1.....	44.4	39.0	39.5
	M-2.....	14.6		
	M-3.....	98.9	106.2	135.0
	M-4.....	40.0	123.9	74.3
	M-5.....	41.0	56.0	
	M-6.....	18.0		
	M-7.....	6.0	27.3	68.7
	M-8.....		64.3	84.5

Despite the markedly improved abundance of whitefish in the State of Michigan waters of Lake Michigan in 1941 and 1942, fishing intensity was relatively low. For the eight districts combined (table 60) the intensity, which was lower in 1940 (55.6 percent) than in any year except 1936 (55.1 percent) of the period, 1929-1939, decreased even further in 1941 (51.8 percent) and remained at about the same level (52.0 percent) in 1942. Among the individual districts (table 59) fishing intensity tended to be rela-

tively high in M-2, M-3, M-4, and M-5 and low in southern Lake Michigan (M-6, M-7, and M-8) and Green Bay (M-1).

The significance of the most recent figures for the whitefish fishery of the State of Michigan waters of Lake Michigan may be summarized in the one statement that the abundance of whitefish appears to be returning to an approximately normal level while production is held in check by a low fishing intensity.

Whether this statement is equally true for the whitefish of the Lake Michigan waters of other States is not known. Virtually no whitefish production is recorded for Illinois and Indiana in 1940-1942. The Wisconsin statistics (table 57) suggest some improvement in that State. In contrast to the Michigan catch, that of Wisconsin increased in both 1940 and 1941, reaching a relatively high level in 1941, although again in contrast to Michigan's yield, it decreased to approximately the normal level in 1942. With respect to the entire lake (all States) the trend of production is upward, after 2 years of extremely low yields.

BEARING OF THE 1940-1942 STATISTICS OF THE WHITEFISH FISHERIES OF LAKES HURON AND MICHIGAN ON THE VALIDITY OF EARLIER CONCLUSIONS

The 1940-1942 statistics of the whitefish fishery of the State of Michigan waters of Lakes Huron and Michigan do not give the slightest reason for modifying the summary paragraphs at the end of part II of the main body of this paper. In Lake Huron the "collapse of the whitefish fishery" proved to be even more devastating than had been anticipated. The belief that in Lake Michigan the decline of the whitefish was "not disastrous" has been substantiated by the return of the whitefish to nearly normal abundance (91 and 95 percent) in 1941 and 1942.

The contrast between conditions in the whitefish fisheries of Lake Huron and Lake Michigan in 1940-1942 is brought out sharply by the data of table 63 (see also table 22 of part II). In Lake Huron, production and fishing intensity, already at an extremely low level in 1940, continued to decline in 1941 and 1942. Any improvement that did occur in the status of the whitefish was relatively small. The abundance of whitefish was relatively much higher in 1940 in Lake Michigan (63 percent of average) than in Lake Huron (29 percent). Furthermore, the abundance in Lake Michigan rose sharply in 1941 and increased again in 1942. The production of whitefish also increased significantly in 1941 and 1942. Only fishing intensity declined (in 1941) or remained unchanged (in 1942). The supplementary data of this appendix, therefore, support the conclusion that overfishing traceable to deep-trap-net operations brought about the ruin of the whitefish fishery in Lake Huron. Although overfishing admittedly may have occurred in Lake Michigan and may have contributed to the decline that culminated in 1940, this overfishing was much less severe than in Lake Huron and did not carry the level of abundance of whitefish so low as to make rapid recuperation of the stock impossible. In fact, only low fishing intensity prevented nearly normal production of whitefish in Lake Michigan in 1941 and 1942.

TABLE 63.—*Production and abundance of whitefish and the intensity of the whitefish fishery in the State of Michigan waters of Lakes Michigan and Huron*

[Expressed as percentages of the 1929-1939 average]

Lake	Item	Year		
		1940	1941	1942
Michigan.....	Production.....	32	38	46
	Fishing intensity.....	56	52	52
	Abundance.....	63	91	95
Huron.....	Production.....	9	5	4
	Fishing intensity.....	29	13	8
	Abundance.....	29	31	35

